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This is the first number of THE NAUTILUS published by The Bailey-Matthews Shell Museum. All correspondence pertaining to subscriptions, purchase of back issues, and missing issue claims should be addressed to:

Dr. José H. Leal
THE NAUTILUS
P. O. Box 1580
Sanibel, FL 33957 USA

Phone: (941) 395-2233
FAX: (941) 395-6706
e-mail: LEAL@WATER.NET

Beginning with volume 112, Dr. Leal will become Editor-in-Chief of THE NAUTILUS. All new manuscript submissions should be addressed to Dr. Leal at the above address.

Ammonicera in Florida: Notes on the Smallest Living Gastropod in the United States and Comments on Other Species of Omalogyridae (Heterobranchia)

Rüdiger Bieler
Center for Evolutionary and Environmental Biology
Field Museum of Natural History
Roosevelt Road at Lake Shore Drive
Chicago, Illinois 60605, U.S.A.
bieler@fmnh.org

Paula M. Mikkelsen
Department of Invertebrates
American Museum of Natural History
Central Park West at 79th Street
New York, New York 10024, U.S.A.
mikkel@amnh.org

ABSTRACT

The first record of a species of *Ammonicera* in Florida, with an additional record from Yucatan, Mexico, is presented and the gross morphology of the living animal is described for the first time. This smallest living snail in the United States is identified as *Ammonicera minortalis* Rolán, 1992, originally described from Cuba. Comparisons are made with closely similar species, especially *A. japonica* Habe 1972, a possibly conspecific form with known wide distribution in the Pacific Ocean. Various taxonomic problems in the genera *Ammonicera* and *Omalogyra* are addressed, and current composition of the family Omalogyridae is discussed. Lists of currently recognized omalogyrid species in the Atlantic Ocean (including the Mediterranean Sea) are presented.

Key words: Florida Keys, Gastropoda, lower Heterobranchia, *Ammonicera*, *Omalogyra*, Omalogyroidea, Atlantic Ocean, Systematics.

INTRODUCTION

The family Omalogyridae is a poorly known group of extremely small marine snails. Placed in their own superfamily Omalogyroidea, they are currently classified as members of the unresolved "lower heterobranch" gastropods (e.g., Haszprunar, 1988; Bieler, 1992; Healy, 1993). Even the most basic taxonomic and distributional information is sketchy for this group, with most faunistic studies missing or deliberately omitting the usually less-than-one-millimeter size range of the adult shells. The few studies that have concentrated on this group have brought many new species to our attention, such as the recent series of works with excellent scanning electron micrographs by Sleurs of omalogyrids in Papua New Guinea (1983) and in the Republic of Maldives (1985b), by Palazzi (1988) in the Mediterranean and Madeira, and those by Rolán in the Cape Verdes (1991) and Cuba (1992). Whether these areas are exceptional in their high species diversity of omalogyrids is doubtful, although it is surprising that no true omalogyrids were reported in some Caribbean studies that otherwise dealt with minute species (*e.g.*, De Jong & Coomans, 1988; Rios, 1994).

In addition to their small size, omalogyrids have anatomical features that set them apart from caenogastropods with which they were usually grouped. This led to early speculations about their systematic position. Because of their unusual radular characters, G. O. Sars (1878) placed the at the time monotypic family as the only member of his new higher taxon "Prionoglossa," giving it equal rank with other groups such as Taenioglossa and Ptenoglossa. Jeffreys (1859a) thought these animals the only surviving members of the otherwise extinct genus *Euomphalus* Sowerby, 1814. Fretter (1948) showed in a detailed anatomical study that *Omalogyra atomus* (Philippi, 1841) differs greatly from the "prosobranchs" with which it was traditionally placed. Omalogyrids have regained interest in recent years because of their presumed basal position within the heterobranchs (Haszprunar, 1988; Ponder, 1990, 1991). Their exact relationships remain uncertain; recent suggestions (Bandel, 1996; Pacaud & Le Renard, 1996) to combine the Omalogyridae with several other families in a superfamily Architectonicoidea are not supported by anatomical data (Healy, 1993; Huber, 1993).

At the nomenclatural level, certain confusion exists in the literature about the usage of genus-group names such as *Ammonicera* versus *Ammonicerina*, and about the identity and authorship of *Omalogyra*'s type species.

The discovery of an *Ammonicera* species in the Florida Keys, representing the smallest gastropod known in the United States, is here used to summarize existing data on Omalogyridae in the Atlantic Ocean and to address additional taxonomic problems.

ABBREVIATIONS USED

AMNH	American Museum of Natural History, New York, U.S.A.
BMNH	The Natural History Museum, London, United Kingdom
FMNH	Field Museum of Natural History, Chicago, U.S.A.
MLP	Museo de La Plata, Argentina
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain
MNHN	Museo Nacional de Historia Natural, Santiago, Chile
ZMB	Zoologisches Museum, Humboldt Universität, Berlin, Germany
SEM	Scanning Electron Micrograph

RESULTS

Family **Omalogyridae** G. O. Sars, 1878: 215 [as **Homalogyridae**]

(often erroneously credited to Fischer, 1885; *e.g.*, Abbott, 1974)

Genus *Ammonicera* Vayssière, 1893

Ammonicera minortalis Rolán, 1992

(Figures 1–8)

Omalogyra species.—Vokes and Vokes, 1984: 168, figs. 7, 7a (SEM).

Ammonicera minortalis Rolán, 1992: 40, 42, figs. 10, 11 (teleoconch), 13, 15 (protoconch) (all SEM).

Holotype: (MNCN 15.05/6794): shell diameter 0.35 mm; type locality: north of Cuba, Baracoa; holotype from 4 m depth.

Type material studied: 3 paratypes, AMNH 226450, from type locality.

Florida material studied: 2 Florida Keys specimens collected and observed alive, one each from station FK-045 [Indian Key Fill, Mile Marker 79, Monroe County, 24°53′25″N, 80°40′28″W, Gulf side, rocks in 0.5–1 m among *Thalassia/Halodule* seagrasses, 20 September 1996] and station FK-062 [Missouri Key, Mile Marker 39.5, Monroe County, 24°40′29″N, 81°14′21″W, Gulf side of Missouri-Ohio Key bridge, subtidal rocks, 14 April 1997]. Also empty shells from sta. FK-040 [Missouri Key site as above, 12 March 1996], FMNH 279010 (1 shell); FK-057 [Missouri Key site as above, 26 September 1996], FMNH 279011 (10 shells incl. SEM material), AMNH 288137 (5 shells). All localities were fully marine and were sampled by the authors by "rock washing" (brushing and rinsing of rock surfaces).

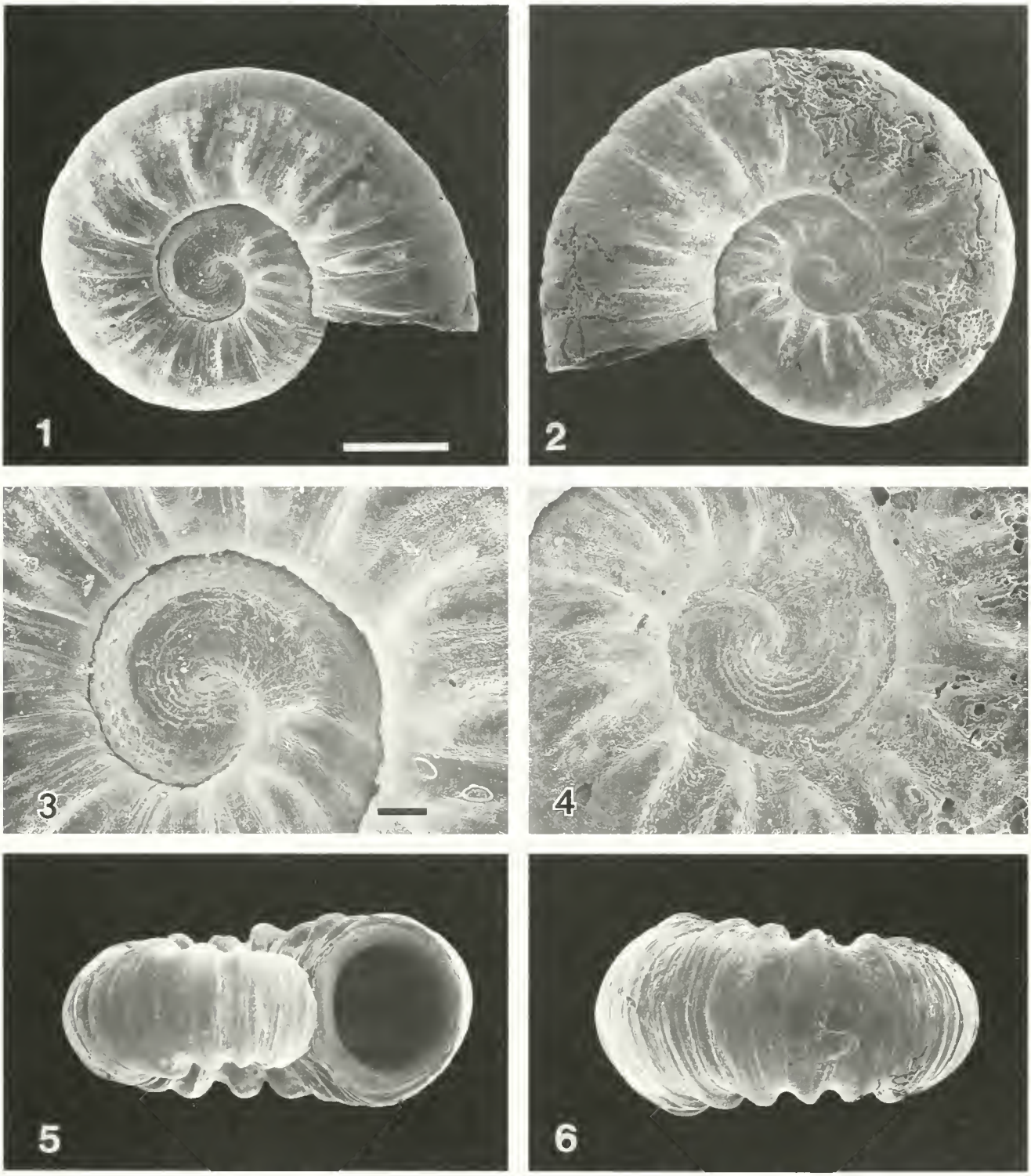
Distribution: Now known from north and south coasts of Cuba (Rolán, 1992), the Florida Keys (this paper), and the Yucatan Peninsula (Vokes & Vokes, 1984).

Description: Shell (Figs. 1–2) extremely minute, diameter 0.34–0.46 mm (0.2–0.4 mm, *fide* Rolán, 1992), planispiral, tightly coiled, glossy, uniformly dark brown, resembling a miniature ammonite in shape and sculpture. Protoconch (Figs. 3–4) of 1.3 whorls[1] (identical in SEM but described as "3/4 whorl," by Rolán, 1992), diameter 120–135 μm, distinctively sculptured with one major spiral cord at mid-whorl, reticulate sculpture peripheral to major cord, and 3–4 smaller spiral ridges central to major cord. No distinction of a separate larval shell ("protoconch II"), indicating the absence of a free swimming larval stage. Coiling near-planispiral, with slight initial hyperstrophy (compare Figs. 3 and 4). Teleoconch of about 1.3 rounded whorls (1–1.5 whorls *fide* Rolán, 1992), sculptured with prominent elongated axial tubercles, regularly spaced, equally sized, beginning immediately after protoconch, numbering 15–19 (13–17 *fide* Rolán, 1992) on body whorl, fading to no axial sculpture at the periphery. Tubercles and spaces between also with fine growth lines. Periphery (Fig. 6) uniformly rounded, smooth except for fine growth lines. No distinct spiral sculpture (but occasionally with extremely fine lines, see specimen in Fig. 1). Outer lip (Figs. 1–2) thin, sharp, ending in a single plane perpendicular to the plane of coiling; aperture circular; columella without folds or grooves. Head-foot (Figs. 7–8) translucent to nearly transparent. Animal gliding rapidly on short foot, with blunt, very active propodium. Shell held nearly vertically as the snail crawls. Transparent operculum on hindfoot serving as a support for the coil of the shell. Head with two finger-shaped tentacles, each held in an erect arch curving toward the midline; eyes black, near base of tentacles. Radula and internal anatomy not studied.

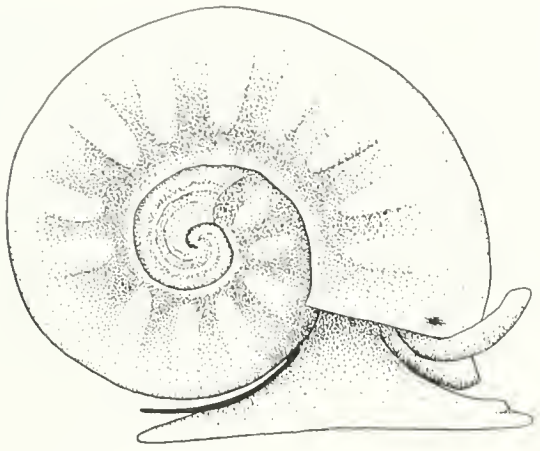
Habitat: Animals not observed *in situ,* but collected from shallow subtidal rocks covered on one or several surfaces with various polychaete worm tubes, marine algae, sponges, tunicates, and numerous other attached or free-living mollusks. Diet unknown (but see below).

Remarks: Although the diet of *Ammonicera minortalis* has not been confirmed, it is likely to feed on the variety of algal species growing in its subtidal rock habitat, based on literature records on the habitat/diet of other Omalogyridae: on *Codium* and *Zostera* (*Omalogyra atomus* [as *Euomphalus nitidissimus*]—Jeffreys, 1859a, 1859d); on *Ulva* (*O. atomus*—Fretter, 1948); on *Fucus* (*A. rota*—Nordsieck, 1972); on *Ulva* and *Enteromorpha* (*O. atomus*—Fretter & Graham, 1978; Graham, 1988); on *Fucus, Laminaria, Cladophora, Corallina, Ulva* (*Ammonicera rota*—Fretter & Graham, 1978); on *Padina* (Hawaiian *A. japonica*—Kay, 1979); piercing algal cells and sucking out the contents, and depositing egg strands on bases of *Cladophora* (*A. rota* /*A. fischeriana*—Franc, 1948; Graham, 1988); on *Halimeda* (*A. japonica* and others—Sleurs, 1985a, 1985c); on *Zostera, Ulva, Cystoseira,* and epiphytic diatoms (*O. atomus, A. fischeriana*—Gaglini, 1993). Bullock *et al.*, 1990, provided the most detailed account, reporting Azorean *O. atomus* and *A. fischeriana* from a variety of algae, including

[1] Ascertained using the method of Taylor as summarized by Jablonski & Lutz (1980: 330, fig. 4)



Figures 1–6. *Ammonicera minortalis*, shells by scanning electron microscopy (four different shells, FMNH 279011). **1.** Apical view. **2.** Umbilical view. **3.** Protoconch (detail of fig. 1). **4.** Protoconch (detail of fig. 2). **5.** Apertural view. **6.** Dorsal view (from "above," as seen in crawling animal). Scale bars: Fig. 1 = 100 μm (Figs. 2, 5, 6 at same scale); Fig. 3 = 20 μm (Fig. 4 at same scale).



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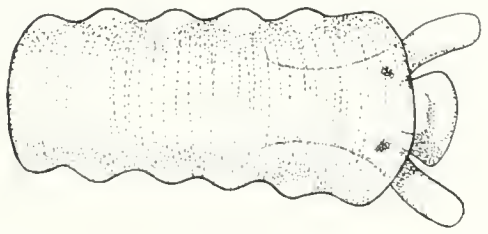

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Figures 7–8. *Ammonicera minortalis*, sketch of living animal. Maximum shell diameter = 0.42 mm. **7.** Right lateral view. **8.** Dorsal view.

Enteromorpha, Cystoseira, Ulva, Pterocladia, Peysonnelia, Halopteris, Asparagopsis, as well as *Codium. Omalogyra atomus,* which they also found on *Gelidium* and *Sargassum,* was the dominant species on *Chondria* and the only mollusk found on *Fucus* in that study.

DISCUSSION

Species-level identification: Rolán (1992) described this species based on empty shells collected from north and south coasts of Cuba (3–20 m). A comparison with the excellent original illustrations and with paratypic material at AMNH proved the identity of the Florida Keys specimens. No other known Atlantic species combines such axial teleoconch sculpture with reticulated sculpture of its protoconch. Rolán apparently was unaware of an earlier record of this form, as "*Omalogyra* species," by Vokes and Vokes (1984) who collected it in Arrecife Alacran, about 140 km north of Progreso, Yucatan, in the Gulf of Mexico.

According to Rolán (1992: 42), only *Ammonicera japonica* Habe, 1972, described as "Japan's smallest gastropod" from Honshu, is "superficially similar but it has very constant spiral striae." Habe's species (1972:115–116, figs. 1–4) was described as 0.42–0.68 mm in diameter, dark brown in color, with "about 16 annulations in the body whorl" (Habe, 1972:116). Habe did not mention or illustrate the spiral sculpture noted by Rolán. Additional specimens were described and illustrated as *Ammonicera japonica* from Hawaii by Kay (1979:92, figs. 32A-C [SEM], as *Omalogyra*; earlier reported by Kay & Switzer, 1974:278, table 1, from Fanning Island). Kay mentioned sculpture "from 16 to 18 axial ribs on the last whorl, the ribs becoming obsolete at the periphery." Spiral striae were not described but faint spiral sculpture is visible in one illustrated shell (Kay, 1979:fig. 32B). Sleurs' (1985a:4–5, pl. 1, figs. 1, 6, 9 [SEM]; as *Omalogyra*) description of *A. japonica* from Papua New Guinea was very similar. He described the protoconch in detail "with reticulated sculpture at the abapical side" (his fig. 9); spiral sculpture of the 0.3 to 0.45 mm large teleoconch was not discussed, but shows very faintly in one SEM illustration (his fig. 6). Fukuda's illustration of this species from the Ogasawara (Bonin) Islands (1994:pl. 35, fig. 697a-e; as "*Omalogyla*" *japonica*), shows no spiral sculpture. The large specimen illustrated (0.4 mm) has about 19 axial ribs.

The protoconch and teleoconch sculpture of the shells of *Ammonicera minortalis* and *A. japonica* are extremely similar according to the SEMs provided by Rolán (1992), Kay (1979), Fukuda (1994) and Sleurs (1985a), respectively, and suggest synonymy of the Caribbean and Indo-Pacific species. Faint spiral teleoconch sculpture appears to occur in some individuals of both nominal species. However, the disjunct distributional pattern makes further study necessary. No similar form has been described or recorded from the eastern Pacific (Shasky, 1989).

As also noted by Rolán (1992), *Ammonicera minortalis* is similar to the European *A. rota* (Forbes & Hanley, 1850) in its teleoconch characters (but the latter has a greater number of whorls and axial tubercles continuing over the periphery). *Ammonicera rota* has, however, a very different protoconch without reticulated sculpture (see, *e.g.*, Rodriguez Babio & Thiriot-Quiévreux, 1974: pl. 2, F-H; as *A. fischeriana*). Also similar is *A. plicata* Sleurs, 1985, from the Maldives (1985b:20 ff., figs. 2, 7, 10, 13, 14), which has a larger teleoconch (0.45 to 0.65 mm) with weaker axial ribs and a protoconch lacking the reticulate sculpture present in *A. minortalis* and *A. japonica*.

Genus-level identification: Omalogyridae currently comprises three recognized extant genera: *Ammonicera* Vayssière, 1893, *Omalogyra* Jeffreys, 1859, and *Retrotortina* Chaster, 1896. The last (with type species by monotypy: *R. fuscata* Chaster, 1896) has a sinistral teleoconch that distinguishes it from *Ammonicera* and *Omalogyra*.

Bandel (1988:9) also placed *Orbitestella* Iredale, 1917, in this family, but Ponder (1990) showed that this genus belongs in the Valvatoidea, not Omalogyroidea. Bandel (1988), who viewed omalogyrids as small-bodied members of Architectonicidae or Architectonicoidea (pp. 10, 17), attempted to introduce a new fossil genus "*Neamphitomaria,*" but did not designate a type species. Bandel (in Dockery, 1993:92) subsequently provided such a

designation (the Upper Cretaceous *Pseudomalaxis stantoni* Sohl, 1960) and thus validated *Neamphitomaria* of that date [not as of 1988 as is frequently cited; see ICZN Art. 13(b)]. *Amphitomaria* Koken, 1897, and *Neamphitomaria* Bandel, 1993, were then placed in a new family, Amphitomariidae, by Bandel (1996), thus removing the genus again from the Omalogyridae.

The placement of the present species in the genus *Ammonicera*, rather than *Omalogyra*, is here accepted because of: (1) its protoconch sculpture with strong spiral ribs and grooves (in contrast to small tubercles in *Omalogyra*; *e.g.*, Rolán, 1992); (2) the presence of distinct cephalic tentacles (absent in *Omalogyra*); and (3) its strong teleoconch sculpture (absent or weak in *Omalogyra*). The known radulae of *Omalogyra* and *Ammonicera* (not yet studied for *A. minortalis*) are so different between members of the two nominal genera that Sleurs (1985c:181) suggested that they might belong to different families. However, published radular data differ even within the two genera: *Omalogyra* radulae have been described as either uniserial (Jeffreys, 1859, 1867; Thiele, 1929; Sleurs, 1985c) or with a formula of 1–1-1 (G. O. Sars, 1878; Thiele, 1929; Egorova, 1991). Those of *Ammonicera* have been described with a formula of 1–1-1 (Vayssiére, 1893) or 1–1–0–1–1 (Sleurs, 1985b, c), and so definitive conclusions must await a detailed comparative study.

Unfortunately, the taxonomic history of *Ammonicera*, *Omalogyra*, and their included species is exceedingly complex and confused (see discussion below).

REMARKS ON *AMMONICERA* AND ITS TYPE SPECIES

Ammonicera was introduced by Vayssière (1893:16 ff.) for *Homalogyra fischeriana* Monterosato, 1869. He provided a full anatomical description based on histology and studies of the radula. Franc (1948:142 ff.) and Sleurs (1985a:9) questioned the identity of Vayssière's material, assuming that his work was based on misidentified "*Omalogyra rota*" Forbes and Hanley, 1850. Compared to Gaglini's descriptions and illustrations (1993:933–04, 934–03–04), Vayssière's line drawings of the shell (1893: figs. 8–9) seem to represent typical *A. fischeriana* in color pattern and relatively fine crenulations of the periphery, although the sketched pronounced axial ribbing is more representative of the nominal species *A. rota*. Monterosato himself considered the two nominal species as varieties of one (*e.g.*, Monterosato 1872:38; 1875:29), and many recent authors (*e.g.*, Fretter & Graham, 1978; Backeljau *et al.*, 1984; Knudsen, 1995) have deemed them synonymous (see also Höisaeter, 1968; van Aartsen *et al.*, 1984). Gaglini (1993), on the other hand, argued convincingly for the presence of two sympatric species. Whether or not they will prove to be synonymous, they are without doubt so closely related and morphologically similar that it will not impact interpretation of the nominal genus *Ammonicera* (in contrast to Sleurs, 1985a).

In addition to Vayssière's extensive description, published biological information about this/these species includes description of gross anatomy (Franc, 1948), nervous system (Huber, 1993), egg capsules (Franc, 1948 [summarized by Knudsen, 1995]; Graham, 1988), and feeding (Graham, 1988).

Ammonicera should not be confused with *Ammonicerina*—see synonymy of *Omalogyra* (below).

REMARKS ON *OMALOGYRA* AND ITS TYPE SPECIES

Omalogyra was introduced by Jeffreys (1859b) in the midst of an engaged discussion (with Clark, 1859) ultimately involving the identities of *Helix nitidissima* Adams, 1800, "*Skenea*" *nitidissima sensu* Forbes and Hanley, 1850, and "*Truncatella*" *atomus* Philippi, 1841. The current understanding of *Omalogyra* is based on Fretter's (1948) excellent anatomical study on British animals identified as *O. atomus*. Other published information on this species includes gross anatomy and radula (G. O. Sars, 1878), nervous system (Huber, 1993), spermatozoa (Healy, 1993), and egg capsules (Graham, 1988; Knudsen, 1995 [However, it should be noted that the accompanying SEM shell photographs, Knudsen's fig. 5, seem to be of a skeneopsid, not of *O. atomus*]). The "eggs" of *O. atomus* as described by Jeffreys (1867) and Lebour (1937) were subsequently recognized as misidentified glandular structures (Fretter, 1948).

No type material for any of these nominal taxa could be located; our following discussion thus has to concentrate on literature review: *Helix nitidissima* J. Adams, 1800, was introduced with a short description and three illustrations (here reproduced in Fig. 9). The species was accepted and cited, in various generic combinations, by subsequent authors (*e.g.*, Weinkauff, 1868:266, as "*Spira nitidissima* Adams"). Many authors have considered *H. nitidissima* J. Adams, 1800, as synonymous with *Truncatella atomus* Philippi, 1841 (*e.g.*, Fischer, 1857; Weinkauff, 1868; Fretter & Graham, 1978; Rolán, 1983; Graham, 1988; Poppe & Goto, 1991; Rosenberg/Malacolog, 1997). The original description by Adams (1800: 4, pl. 1, figs. 22–24) was based on the shell alone: "H.[elix] testa duobus anfractibus, subtilissime transverse striata. Obs. Corneous, pellucid, umbilicated; easily distinguished by the uncommon brilliancy of its glossiness." Original figure 23, said to be of "natural size" (1800:6) measures nearly 3 mm. The shell, much too large to be a European omalogyrid species, was subsequently recognized as "evidently the fry of *Zonites radiatulus* [J. Alder, 1830]," a land snail, by Jeffreys (1867:71). The holotype of *H. nitidissima* was not located (K. Way, BMNH, pers. comm., 1997). The interpretation as a young stage of a British land snail is here accepted; *H. nitidissima* Adams is not a senior synonym of *T. atomus*.

Much of the interpretation of "*nitidissima* " by subsequent authors was based on "*Skenea*" *nitidissima sensu* Forbes and Hanley, 1850, who used this name for a different species. Several authors erroneously credited Forbes and Hanley with the description of a new species

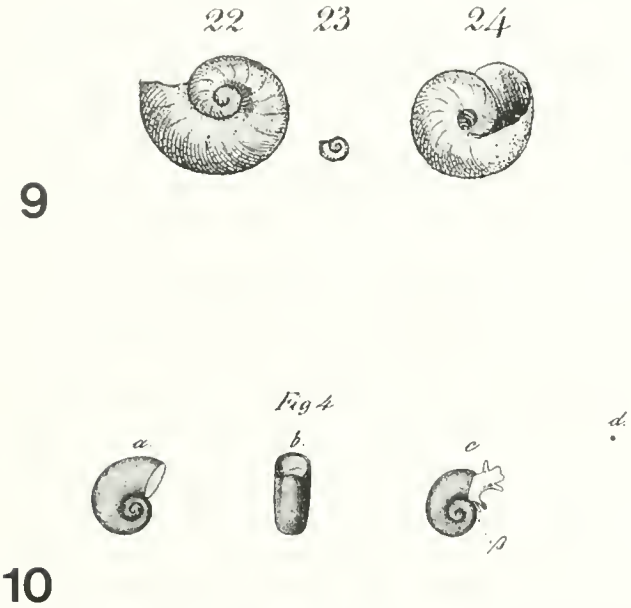

Figure 9. Reproduction of original illustrations of *Helix nitidissima* J. Adams, 1800 (from Adams, 1800: pl. 1, figs. 22–24).

Figure 10. Reproduction of original illustrations of *Truncatella atomus* Philippi, 1841 (from Philippi, 1841: pl. 5, figs. 4a-d).

"*Skenea nitidissima* " (e.g., Jeffreys, 1860; Nordsieck, 1972; Nordsieck & Garcia-Talavera, 1979; Gaglini, 1993). However, Forbes and Hanley themselves (1850: 158) cited the species as "*S.[kenea] nitidissima*, Adams" with full page and figure reference to Adams' original work. It is this misidentified "*nitidissima sensu* Forbes & Hanley" that enters into the various lengthy published discussions comparing "*nitidissima*" and *Truncatella atomus*.

Philippi (1841:54, pl. 5, figs. 4a-d) described and illustrated *Truncatella atomus*, collected in Sorrento (Campania, southern Italy). He emphasized that he was able to study the animal in detail at a magnification of 60 times and placed it in *Truncatella* because of the animal's similarity to members of that genus. In 1844, he re-described the species (p. 134, pl. 24, fig. 5; again as "n. sp.") and reproduced his 1841 illustrations of *T. atomus*. Philippi's (1841) illustrations, here reproduced in Fig. 10, show a living specimen with planispiral shell (with logarithmic growth), tapering tentacles, an operculum, and a representation of actual size of about 0.5 mm. The type material has not been located in Berlin or Santiago (von Rintelen, ZMB, pers. comm., 1997; MNHN, pers. obs., 1997).

Forbes and Hanley (1850:158–160, pl. 73, figs. 7, 8) described and illustrated a British shell under the name "S.[*kenea*] *nitidissima*, Adams"; they did not mention the living animal. They placed Philippi's *Truncatella atomus*, with question mark, in synonymy. Jeffreys (1859a:109–111, pl. 3, figs. 15a, b, 16a-c) discussed the species, as *Euomphalus nitidissimus*, with a sketch of the animal (showing ciliated head lobes, no tentacles, and a uniseriate radula). He reported its range as "from the Shetlands to Sicily, and probably far beyond these limits" (p. 111) based in part on the synonymy of *Truncatella atomus* of Philippi, and expressed his astonishment over Philippi's "mistake" of describing the animal so differently (*i.e.*, with tapering tentacles).

Much of the ensuing confusion was based on (1) the treatment of Philippi's Italian "*Truncatella atomus*" specimens as members of the British "*Omalogyra nitidissima*" *sensu* Forbes and Hanley, and (2) the discrepancy between gross anatomical descriptions of these two species, *i.e.*, with or without tapering head tentacles, respectively.

Clark (1859:410–413, text-figure), after reexamining British animals reconstituted from dried specimens, disagreed with Jeffreys and corroborated the correctness of Philippi's figure of an animal with triangular tentacles, the large eyes embedded at the center of their bases. "It appears quite clear that Mr. Jeffreys has delineated his animal with rounded lobes, or, in other words, with the tentacles retracted. . ." (p. 411). Jeffreys (1859b:498) rebutted: "What Mr. Clark supposed to be tentacula must have been the shrivelled lobes of the veil. . .." Fischer (1859:364–367) joined Clark in criticizing Jeffreys (1859c), assuming that the latter had described a larval stage with vela instead of tentacles. Jeffreys then (1860: 108–111), in rebuttal of Fischer, affirmed that his observations were based on adult specimens without tentacles. Finally, in British Conchology, Jeffreys (1867:67–71, pl. 1, fig. 5; 1869:209, pl. 70, fig. 2) again described the shell and animal in detail, reaffirming his opinion of Philippi's error, but recognized the priority of "*Homalogyra atomus*" (Philippi) over "*Skenea nitidissima*" of Forbes and Hanley. This "anatomically corrected" *Homalogyra atomus*, with "*Skenea*" *nitidissima sensu* Forbes and Hanley in synonymy, is the *Omalogyra atomus* described in detail by Fretter (1948) and that currently forms our concept of the genus.

Unfortunately the original figures of *Truncatella atomus* Philippi, 1841, are in conflict with the descriptions of Fretter. Philippi's illustrated gross morphological details (*i.e.*, tapering tentacles) are indicative of *Ammonicera*. Meanwhile, the sketched smooth shell appears in line with the current concept of *Omalogyra*. In the absence of type material, it is impossible to explain this discrepancy. It is possible that Philippi's material contained members of both genera and his illustration is a composite based on more than one species.

In the interest of nomenclatural stability, we base our interpretation of Philippi's *Truncatella atomus* on his illustration/description of the shell alone (excluding the anatomy in original fig. 4c), thus preserving this name for "*Skenea*" *nitidissima sensu* Forbes and Hanley, 1850 (non Adams, 1800), and *Omalogyra atomus sensu* Jeffreys, 1859, as well as Fretter, 1948.

The taxonomic confusion has been compounded by uncertainty about the type species designation and the date of introduction of *Omalogyra*. Some authors (*e.g.*,

Warén, 1980:12) cited it as having been introduced by Jeffreys (1860), with type species *Truncatella atomus* Philippi, 1841, by monotypy. Others (*e.g.*, Wenz, 1939: 647–648) gave "*O. nitidissima* (Forbes & Hanley)" as type species. The date of description is often erroneously cited as "1867" (*e.g.*, Abbott, 1974; Castellanos, 1989a; Vaught, 1989; Rios, 1994).

The generic name "for the reception of these anomalous mollusks" was in fact proposed by Jeffreys (1859b: 498). In that paper, he referred by name to "*Euomphalus nitidissimus*" (with reference to his earlier, 1859a, article), to "*E. Rota*" and its "variety *tricarinata* of Webster." In the referenced article, he additionally stated a synonym for "*E.*" *nitidissimus*: "I have no doubt that it is the *Truncatella atomus* of Philippi" (1859a:111). Jeffreys did not indicate a type species. Following ICZN (1985: Art. 69(i)), there are four "originally included nominal species":

Helix nitidissima J. Adams, 1800. Now considered a land snail [Jeffreys recognized the misidentification only in 1867; his (1859a, b) usage thus cannot be construed as "deliberately used in the meaning of a previous misuse" (ICZN, 1985: Art. 11(i)].

Truncatella atomus Philippi, 1841 [in synonymy].

Skenea rota Forbes and Hanley, 1850. Now considered a member of *Ammonicera*

Skenea tricarinata Webster, 1856. Described as a potential new species; subsequently (beginning with Jeffreys in Webster, 1857) considered a variety/synonym of *S. rota*

Jeffreys (1867:69 ff.) synonymized "*Skenea nitidissima*" *sensu* Forbes and Hanley under *Truncatella atomus*, after recognizing the true *Helix nitidissima* Adams as a land snail. He also synonymized *Skenea tricarinata* Webster under *Skenea rota*. No type species was designated. Jeffreys therein changed the generic name to *Homalogyra*, an unjustified emendation. The first authors to select a type species appear to have been Bucquoy *et al.* (1884:78) who stated "Type: *Homalogyra atomus* Philippi sp. (*Truncatella*)."

We therefore offer the following synonymies:

Omalogyra Jeffreys, 1859b:498; type species by subsequent designation of Bucquoy *et al.* (1884:78), *Truncatella atomus* Philippi, 1841

Ammonicerina O. G. Costa, 1861: 71; type species by subsequent designation of Dall (1927b:134, as "*Ammonocerina*"), *Ammonicerina simplex* O. G. Costa, 1861. Preoccupied by *Ammonicerina* O. G. Costa, 1856 [Protista]. This taxon is usually placed in synonymy of *Ammonicera* (*e.g.*, Palazzi & Gaglini, 1979); however, its type species by subsequent designation belongs to *Omalogyra*.

Homalogyra Jeffreys, 1867:67 (an unjustified emendation).

Note: In the description of their new genus *Transomalogyra*, Palazzi and Gaglini (1979:33) made *Ammonicerina simplex* O. G. Costa, 1861, the type species by original designation. This would make *Transomalogyra* an objective synonym of *Ammonicerina* and a subjective synonym of *Omalogyra*. However, as pointed out by Warén (1991:74), the type species was misidentified, with Palazzi & Gaglini's illustration actually showing a shell of *Adeuomphalus ammoniformis* Seguenza, 1876. Warén (1991) thus placed *Transomalogyra* in the synonymy of *Adeuomphalus* Seguenza, 1876, as a genus *incertae sedis* in the "Archaeogastropoda."

Omalogyra atomus (Philippi, 1841)

Truncatella atomus Philippi, 1841:54, pl. 5, fig. 4a-d [excluding the sketched animal in fig. 4c].

Skenea nitidissima (Adams) *sensu* Forbes and Hanley, 1850, *et auct.* [*non Helix nitidissima* J. Adams, 1800].

Homalogyra atomus var. *vitrea* Jeffreys, 1867:69.

Homalogyra atomus var. *fasciata* Monterosato, 1877:418.

Notes on other named "varieties":

Homalogyra atomus var. *maculata* Dautzenberg and Durouchoux, 1914:27. The authorship of this name is usually credited to Monterosato, 1875 (*e.g.*, Gaglini, 1993: 928–02). However, Monterosato's applications and some subsequent citations of the name are not available for nomenclatural purposes because they represent *nomina nuda* (Monterosato, 1875:29; 1878:88; Bucquoy *et al.*, 1884:324). The first available introduction appears to be that of Dautzenberg and Durouchoux (1914).

Ammonicerina atomus "var. *pallida* Monterosato 1884" as cited by Gaglini (1993:928–02) is likewise not available as of that date. Monterosato's usage (1884:22) of "var. *pallida*" is a *nomen nudum*, as is his *Homalogyra atomus* var. *zonata* Monterosato (1878:88), subsequently cited as "var. ex colore 2, *zonata* Monts." by Bucquoy *et al.* (1884:324; likewise a *nomen nudum*).

Homalogyra atomus var. *nautiliformis* De Gregorio, 1889, was recognized by Monterosato (1890:141) as a juvenile of *Capulus ungaricus* (Linnaeus, 1758). Nevertheless, the name *nautiliformis* De Gregorio, 1889, was retained by some authors to describe an *Omalogyra* morph with a much widened body whorl (*e.g.*, Nordsieck, 1972:148; Gaglini & Curini Galletti, 1978:210, fig. 2c). Gaglini (1993:928–02–3) introduced a new infrasubspecific name for this morph, *Omalogyra atomus* var. "*inflata*."

Homalogyra atomus var. *polyzona* "Brusina mss. (fide Monterosato)" in Bucquoy *et al.*, 1884:324, pl. 37, fig. 32. Earlier references to a variety "*polyzona* Brusina" by Monterosato (1872; 1875; 1878) are unavailable because they were stated in synonymy or as *nomina nuda*. Gaglini (1993:931–01, 931–02–3) showed that this is a potential synonym of *O. simplex*, not *O. atomus*.

CURRENT COMPOSITION OF OMALOGYRIDAE

Recognized western Atlantic Species: [regions of type localities in brackets]

Ammonicera albospeciosa Rolán, 1992:44, figs. 17, 19, 21 [Cuba]

Ammonicera circumcirra Rolán, 1992:45, figs. 23, 26, 28 [Cuba]
Ammonicera familiaris Rolán, 1992:42, 44, figs. 16, 18, 20 [Cuba]
Ammonicera lineofuscata Rolán, 1992:44–45, figs. 22, 24–25, 27 [Cuba]
Ammonicera minortalis Rolán, 1992:40, 42, figs. 10–11, 13, 15 [Cuba]
Ammonicera sculpturata Rolán, 1992:40, figs. 9, 12, 14 [Cuba]
Omalogyra atomus (Philippi, 1841:54, pl. 5, figs. 4a-d) [Mediterranean]
Omalogyra burdwoodiana (Strebel, 1908:52, pl. 6, fig. 85a-c [Burdwood Bank, south of Falkland Islands]
Omalogyra fuscopardalis Rolán, 1992:36, 38, figs. 1, 3, 5, 7 [Cuba]
Omalogyra taludana Castellanos, 1989a:88–89, figs. 1, 2 (plus sketch of apertural aspect in 1989b:pl. 1, fig. 10) [off San Jorge Gulf, Argentina]
Omalogyra zebrina Rolán, 1992:38, figs. 2, 4, 6, 8 [Cuba]

For the western Atlantic, eleven omalogyrid species are currently recognized. Of these, eight are to date only known from Cuba (all described by Rolán, 1992). Two others, *Omalogyra burdwoodiana* (Strebel, 1908) and *O. taludana* Castellanos, 1989, are known from subantarctic waters off South America. Two omalogyrid species are now recognized from the east coast of the United States: *Ammonicera minortalis* and *O. atomus*.

Several other nominal omalogyrid species have been reported for the western Atlantic Ocean, but need to be excluded from that fauna:

"*Omalogyra planorbis*": A nominal species in the western Atlantic frequently cited as an omalogyrid is *Lippistes? planorbis* Dall, 1927a:131, originally described from "off Fernandina," Florida. This deep-water species was re-described in detail by Moore (1971: 114–116, fig. 1) as *Omalogyra planorbis*, and subsequently called *Omalogyra (Ammonicera) planorbis* (*e.g.*, Abbott, 1974:81; Rios, 1994:60). This taxon was placed in *Palazzia* Warén, 1991, as an "archaeogastropod" group of uncertain affiliations, tentatively assigned to Skeneidae (Warén, 1991: 74, 76).

"*Ammonicera fischeriana*": Nordsieck (1972:149) referred to "*Ammonicera fischeriana* (Monterosato, 1869) = *densecostata* [sic] (Jeffreys, 1884)" in "Westindien," without further explanation. This synonymy is erroneous. The West Indian record for this Mediterranean species is based on Watson's (1886) "Challenger" material of "*densicostata*" as explained in the following.

"*Omalogyra (Ammonicera) densicostata*": *Homalogyra densicostata* Jeffreys, 1884:129, pl. 10, fig. 1, was described from "Porcupine" stations (1098–2002 m) off the coast of Portugal. Additional material from a "Bulldog" cruise off Labrador (2967 m) was also included in the original description. Abbott (1974:81) reported this species as *Omalogyra (Ammonicera) densicostata* from deep water off Portugal, the Azores, and Labrador. Moore (1971:114) showed that the Labrador ("Bulldog") material in fact belongs to "*Lippistes*" *planorbis* Dall, 1927, thus removing the Labrador record for "*O.*" *densicostata*. Watson (1886:677) added a "*Homalogyra densicostata* (?)" record from north of the island of Culebra, between Puerto Rico and the Virgin Islands ("Challenger" station 24, 715 m). Moore (1971:115–116) doubted both the synonymy of the Challenger material and that of the shallow-water material reported by Dautzenberg (1889:46) for the Azores, thus restricting *densicostata* again to the eastern Atlantic. The species was considered a member of the eastern Atlantic omalogyrid fauna until recently (*e.g.*, Sabelli et al., 1990; Gaglini, 1993). *Homalogyra densicostata* was synonymized under *Adeuomphalus ammoniformis* Seguenza, 1876, and placed as an "archaeogastropod" of uncertain affiliations, tentatively assigned to Skeneidae (Warén, 1991:74 ff.).

Recognized eastern Atlantic/Mediterranean Species: [regions of type localities in brackets]

Ammonicera burnayi Rolán, 1991:112, figs. 13–14 [Cape Verde Archipelago]
Ammonicera fischeriana (Monterosato, 1869:274–275, pl. 13, fig. 1) [Mediterranean]
Ammonicera lignea (Palazzi, 1988:105, figs. 8, 18) [Madeira]
Ammonicera multistriata Rolán, 1991:112, 114, figs. 15–16 [Cape Verde Archipelago]
Ammonicera nolai Rolán, 1991:110, figs. 8–9 [Cape Verde Archipelago]
Ammonicera oteroi Rolán, 1991:110, 112, figs. 10–12 [Cape Verde Archipelago]
Ammonicera robusta Rolán, 1991:114–115, figs. 17–18 [Cape Verde Archipelago]
Ammonicera rota (Forbes & Hanley, 1850:160, pl. 73, fig. 10; pl. 88, figs. 1, 2) [Ireland]
Ammonicera rotundata (Palazzi, 1988:105, figs. 10, 21, 27) [Madeira]
Ammonicera verdensis Rolán, 1991:109, figs. 6–7 [Cape Verde Archipelago]
Omalogyra atomus (Philippi, 1841:54, pl. 5, figs. 4a-d) [Mediterranean]
Omalogyra disculus Palazzi, 1988:104, figs. 1, 20 [Madeira]
Omalogyra simplex (O.G. Costa, 1861:72, pl. 11 figs. 3 a, b) [Mediterranean]
Omalogyra undosa Palazzi, 1988:104, figs. 5, 15 [Madeira]
Retrotortina fuscata Chaster, 1896:2 [Strait of Gibraltar]

In the eastern Atlantic, fifteen omalogyrid species are currently recognized, comprising ten species of *Ammonicera*, four of *Omalogyra*, as well as *Retrotortina fuscata* (for Mediterranean records see also Sabelli *et al.*, 1990; Le Renard *et al.*/CLEMAM, 1997). *Omalogyra atomus* is the only species known from both sides of the Atlantic; it is widely distributed, ranging from the Mediterranean, Madeira, and the Azores to Norway, Iceland, Greenland, and in New England (Abbott, 1974; Bullock, 1969, 1995; Fretter & Graham, 1978; Thorson, 1944) from Maine to Rhode Island. Egorova (1991) recognized material from Antarctic waters, previously identified and cited as *O. atomus*, as members of a morphologically extremely similar species, *O. antarctica* Egorova, 1991.

Several other nominal omalogyrid species have been described for the eastern Atlantic. Of these, *Omalogyra aperta* Sykes, 1925:192, from off Portugal, was recognized as a member of the "archaeogastropod" genus *Eu-*

daronia Cotton, 1945, by Warén (1991:80). *Homalogyra granulosa* Sykes, 1925, also from off Portugal, was placed in the "archaeogastropod" genus *Retigyra* Warén, 1989 (see Warén, 1992:168). *Homalogyra paradoxa* "Monterosato (? MS.)" of Sykes (1925:192) is a *nomen nudum*. Two other nominal species introduced by Sykes (*H. sinuosa* Sykes, 1925, and *H.* (?) *marshalli* Sykes, 1925) are in need of further study (see Palazzi, 1992). An additional Mediterranean species, *O. ausonia* Palazzi, 1988, was recently made the type of *Palazzia* Warén, 1991, and transferred to the "archaeogastropods," with tentative placement in the Skeneidae (Warén, 1991). Nominal species *Homalogyra ornata* Dautzenberg, 1889 (p. 46, pl. 4, fig. 9a-d), described from the Azores, is still in need of reinvestigation.

It should be noted that Palazzi (1988) used "ausonia" (Italy) and "disculus" (little disk) as nouns in apposition in the original descriptions; recent usage as "*Palazzia ausoniae*" or "*Omalogyra discula*" (*e.g.*, Sabelli *et al.*, 1990; Giannuzzi-Savelli *et al.*, 1994; Arduini *et al.*, 1995) are incorrect subsequent spellings.

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Morphology and Systematic Position of *Rissoella caribaea* Rehder, 1943 (Gastropoda: Heterobranchia: Rissoellidae)

John B. Wise
Department of Malacology
Houston Museum of Natural Science
One Hermann Circle Drive
Houston, Texas 77030-1799 USA
E-mail: jwise@hmns.org

ABSTRACT

Rissoella caribaea is one of only three known western Atlantic species of rissoellids. It was first described by Rehder (1943a,b) living amongst algae on the mangrove prop-roots at Bonefish Key, Lower Florida Keys, Florida. *Rissoella caribaea*, like other rissoellids, has a pair of cephalic tentacles and a very distinctive (diagnostic) pair of oral lobes on either side of its bifid snout. It has a rhomboid-shaped jaw, a symmetrical radula, each row comprised of rachidian and one pair each of lateral and marginal teeth. *Rissoella caribaea* is a simultaneous hermaphrodite, with well developed penis, vas deferens and a large portion of the female reproductive tract within the mantle floor. This study supports the allocation of this species to the genus *Rissoella*. However, this assignment is based upon our current and very limited understanding of rissoellid morphology and phylogenetics.

Key words: Heterobranchia, Rissoellidae, *Rissoella*, anatomy.

INTRODUCTION

Rissoella caribaea Rehder, 1943a, one of only three known western Atlantic rissoellid species, occurs from the Florida Keys to Brazil and Puerto Rico (Robertson, 1961a; Abbott, 1974; Rios, 1994). Although the genus has a worldwide distribution, and the family is considered important for developing an understanding of gastropod phylogenetic relationships, the anatomies and life histories of these minute gastropods are poorly understood (Bartsch, 1920; Thiele, 1912, 1925, 1929; Ankel, 1936; Lebour, 1936; Fretter, 1948; Robertson, 1961a, 1985; Fretter & Graham, 1962, 1994; Haszprunar, 1988; Ponder, 1966, 1983; Huber, 1987, 1993; Ponder & Worsfold, 1994; Simone, 1995).

Members of the Rissoellidae are thought to be basal Heterobranchs because they possess the following putative synapomorphies : 1) ciliary tracts located on the right side of the mantle cavity; 2) gonoduct on mantle floor; 3) eye position, posterior to the base of the cephalic tentacles, although Ponder and Yoo, 1977, reported its position to be variable in the family; and 4) sperm morphology (Haszprunar, 1988; Healy, 1993; Warén & Ponder, 1994). Moreover, molecular studies support the hypothesis that the Rissoelloidea are sister taxa to the Pyramidelloidea and other "lower" Heterobranchs (Harasewych *et al.*, 1997).

This study was undertaken to provide further insight into rissoellid anatomy and biology, and more specifically, the assignment of *R. caribaea* to the genus *Rissoella*.

MATERIAL AND METHODS

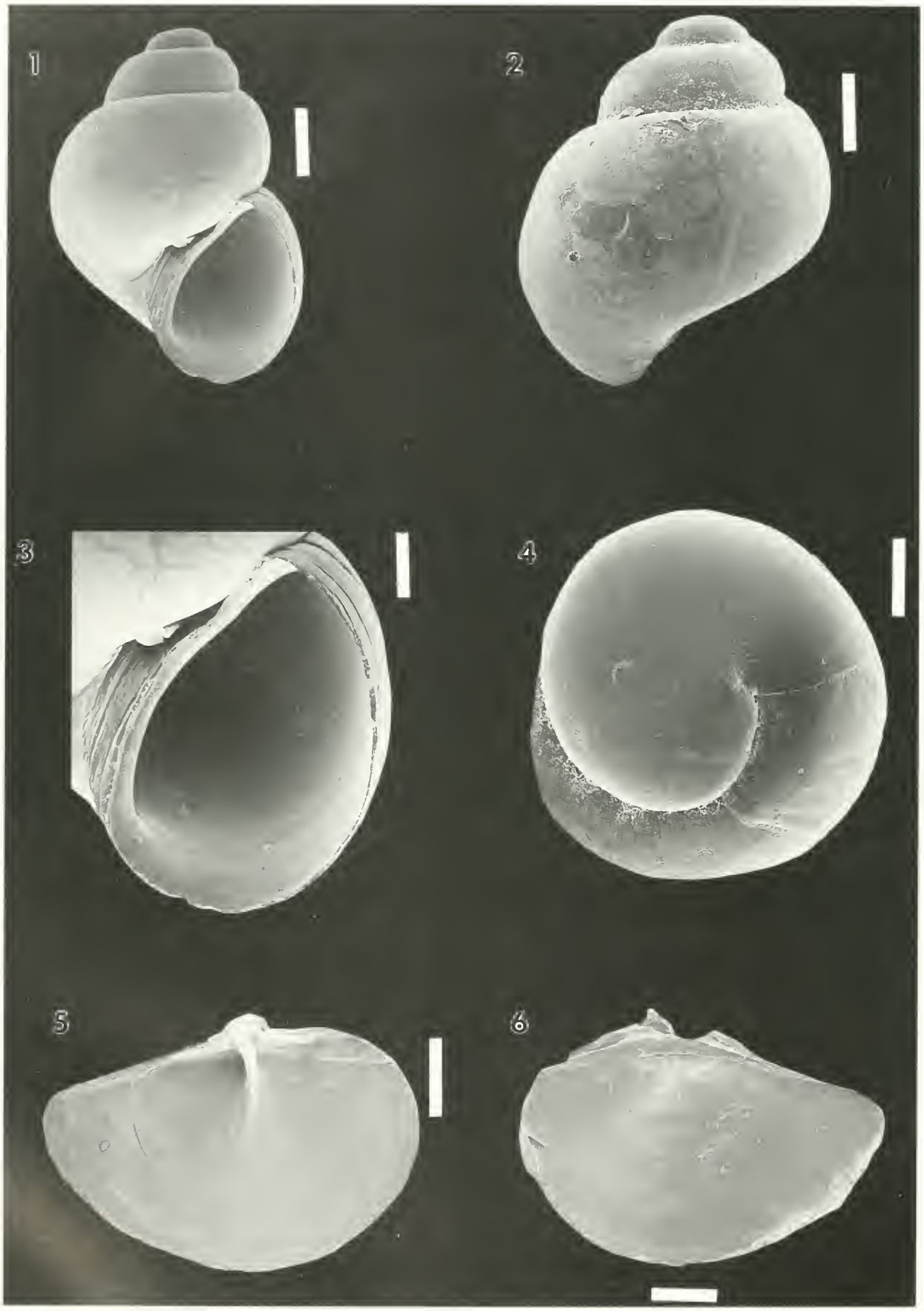
Specimens of *Rissoella caribaea* were collected by washing the tops and often embedded undersides of rocks and coral rubble. Debris was placed in a 0.5 mm sieve, rinsed with seawater to eliminate mud and sand, and sorted under a dissecting microscope. Snails were kept alive in small bowls of aerated seawater.

Living snails were observed and photographed with a Pentax 35mm camera mounted on a Zeiss Tessavar dissecting microscope. Snails were dissected whole, once their shells were cracked with forceps and shell fragments removed. Whole animals and/or their alimentary and reproduction systems (once excised) were stained with toluidine blue. Line drawings were produced using a dissecting microscope with a camera lucida.

Shells were decalcified using a commercial decalcifier (Decalcifying solution, Krajian, J.T. Baker). Specimens were rinsed in 3 changes of seawater and fixed in 10% formalin buffered with filtered seawater. Snails were embedded in paraffin, sectioned at 3–5 μm, and stained with hematoxylin and eosin-Y (Sheehan & Hrapchak, 1980).

Opercula and shells were cleaned by sonication, air dried, coated with gold-palladium and examined with a Cambridge S-650 scanning electron microscope set to 5–10 KEV.

Several specimens were fixed in 2.0% glutaraldehyde buffered in 0.025M sodium cacodylate in filtered seawater. Once fixed, tissues were rinsed with sodium cacodylate buffered/seawater. These specimens were de-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hydrated in a graded series of ethanol, critical point dried, coated and examined with a scanning electron microscope, as above.

Specimens used in this study were collected in the Florida Keys, Florida Bay at Craig Key, Florida (24°50′N, 40°45′W), December 1994; and Fiesta Key, Florida (24°49′N, 80°47′W), October 1996 and February 1997. Identification was confirmed by comparing this material against the holotype of *Rissoella caribaca* (USNM No. 536046). Voucher specimens on deposit at Houston Museum of Natural Science, Houston, Texas. (HMNS Nos. 43688–43690).

SYSTEMATICS

Class Heterobranchia
Family Rissoellidae Gray, 1850
Genus *Rissoella* Gray, 1847

Type species: *Rissoella diaphana* Alder, 1848

Diagnosis: Shell transparent, smooth, broadly ovate to more slender, 1–2 mm in length. Umbilicus broad to narrowly keeled or absent. Aperture ovate to semicircular, with thin outer lip. Protoconch of 1–1.5 dextral whorls. Operculum translucent, corneous, ovate, with ventral peg on columellar side. Head-foot white, yellow, gray or black. Head with pair of cephalic tentacles and pair of oral lobes (= triangular lobes, Fretter, 1948; oral tentacles, Ponder & Yoo, 1977) on either side of bifid snout. Eyes black, often surrounded by clear mound. Nervous system highly concentrated, with fused ganglia and untwisted visceral loop. Mentum absent. Propodium bifurcate. Foot broad anteriorly, tapered posteriorly. Jaw present. Radula variable, with 3, 5, or 7 teeth/row. Rachidian cusps numerous, few or absent. Feeds on diatoms, micro-algae, and detritus. Simultaneous hermaphrodite, with opaque or orange ovotestis along columellar side of visceral mass. Egg capsules hemispherical to ovoid, with 1–2, and rarely 3 eggs. Development direct.

Remarks: For a discussion of the genus and type species see Robertson, 1961b, 1962, and Ponder, 1966, and Ponder & Yoo, 1977.

Rissoella caribaea Rehder, 1943a
Rissoella caribaea Rehder, 1943a: 194, pl. 20, fig. 7. (Holotype:USNM 536046: type locality: Bonefish Key, Florida Keys); Abbott, 1974:723, after Robertson, 1961a.

Description: *Shell* (Figs. 1–4): Globular, transparent, thin, fragile, 1 to 1.8 mm in length, composed of 2 to 3 adult whorls (Figs. 1, 2). Whorls convex, with moderately shallow sutures. Body whorl 75 to 80% of shell length. Teleoconch smooth, with very fine axial growth lines. Umbilicus narrow, with sharp keel. Aperture elongate-ovate (Fig. 3). Protoconch smooth, dextral, with 1.25 whorls (Fig. 4). Operculum ovate, translucent, with peg extending from ridge parallel to columellar opercular edge (Figs. 5, 6).

Head-foot (Figs. 7–9, 11, 12): Head colored with dark brown, reddish brown, or black pigmentation (Figs. 7, 11). Dark brown, gray, or black tentacles oval in cross-section. Oral lobes equal to, or slightly longer than cephalic tentacles. Both tentacles and oral lobes ciliated (Figs. 7, 9, 11). Eyes black, with well developed lenses, posterior to tentacles on unpigmented, slight protuberance (Fig. 11). Snout bifid and bilobed. Mouth vertical slit, medial and ventral to head. Foot broad anteriorly, medially bifurcate, wide, tapering posteriorly. Foot unpigmented, translucent, gray to white. Opaque crescent-shaped ridge on dorsal surface of propodium (Fig. 11). Mentum absent. Ventral surface of foot unpigmented and highly ciliated (Fig. 8). Pedal gland opens along middle of sole, producing a very fine, transparent attachment thread. Opaque visceral mass gray-white or brown, with scattered and/or aggregates of black and/or dark red-brown cells.

Alimentary tract (Figs. 7, 11, 13–19): Gut extends posteriorly from bulbous snout, under mantle floor to stomach, located within visceral mass. Cylindrical stomach wide medially, tapering at junctions of esophagus and intestine. Jaw, consisting of two rhomboidal sections joined together at one of two long sides to form a tent-like structure, just posterior to buccal opening. Jaw covered with numerous, tightly interlocking scales. Radular ribbon approximately 150μm long, 50μm wide, with about 30 rows of teeth (Fig. 13). Radula symmetrical, with large rachidian teeth, each consisting of wide basal portion supporting a laterally rounded upper portion (Fig. 14). Upper portion with medial indentation and numerous fine serrations (Figs. 14, 15). Basal portion of lateral teeth broad, with numerous serrations. Anterior portion hook-shaped, serriform (Figs. 13, 16, 17). Marginal teeth similar to lateral teeth, with broad base and hooked serrated anterior portion, with cuspidate crest (Figs. 18, 19).

Pallial cavity (Figs. 11, 12): Short, spacious pallial cavity. Anterior mantle edge folded, finely crenulate, with black pigmentation arranged as stripes. Pigmented hypobranchial gland (=pigmented mantle organ? *sensu* Robertson, 1985), within mantle roof, exudes copious, thick blue-white exudate that mainly exits right side of

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Figures 1–6. Scanning electron microphotographs of the shell and operculum of *Rissoella caribaea* **1.** Apertural view of shell (scale bar = 200 μm). **2.** Dorsal view of shell (scale bar = 150 μm). **3.** Enlargement of aperture (scale bar = 100 μm). **4.** Apical view of protoconch (scale bar = 50 μm). **5.** Attachment surface of operculum (scale bar = 100 μm). **6.** Outer surface of operculum (scale bar = 100 μm).

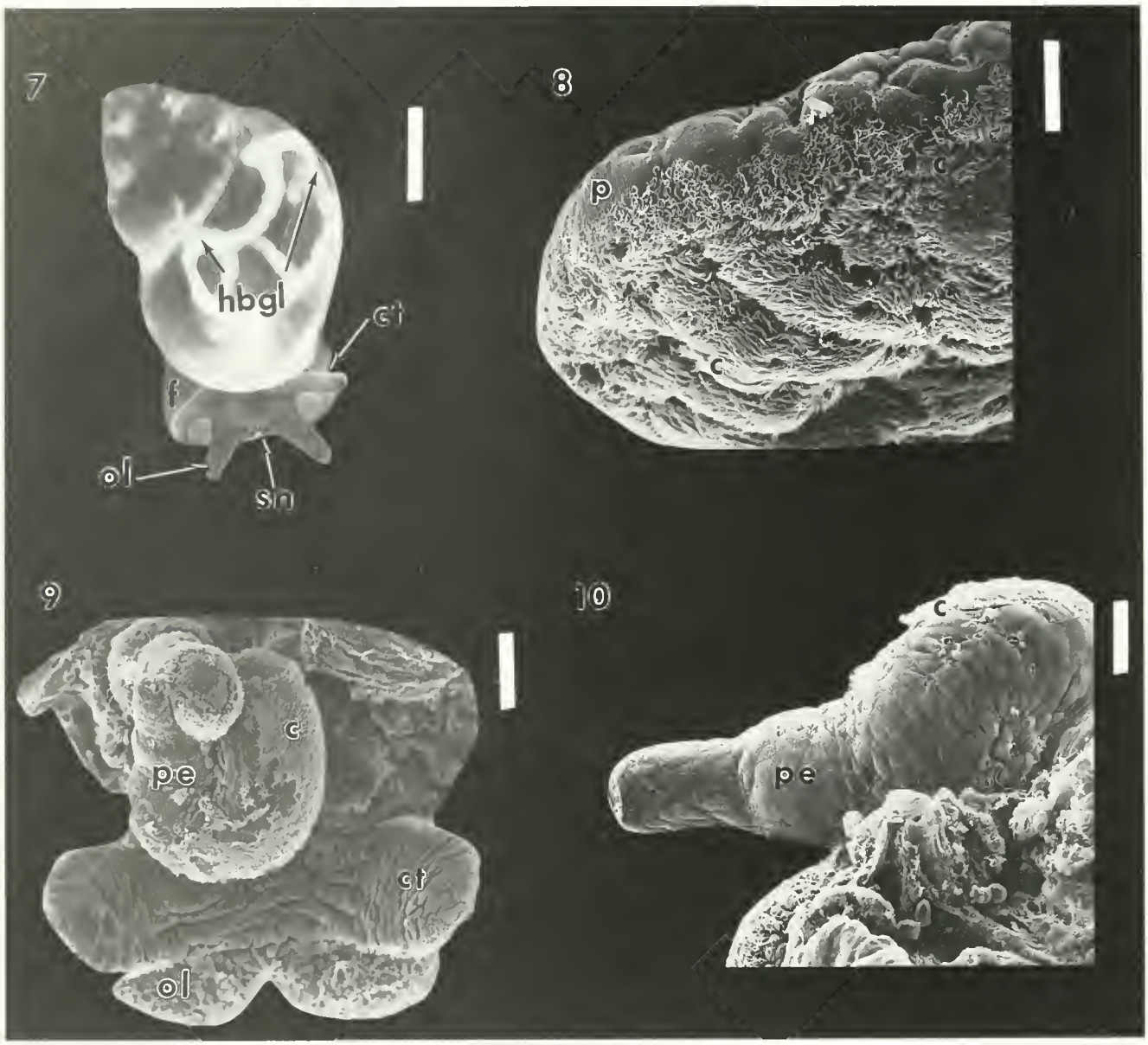

Figure 7. Living *Rissoella caribaea* (scale bar = 250 μm). **Figures 8–10.** Scanning electron microphotographs of critical-point dried *R. caribaea*. **8.** Propodium/sole (scale bar = 25 μm). **9.** Penis on neck posterior to cephalic and labial tentacles (scale bar = 50 μm). **10.** Penis (scale bar = 30 μm) (c = ciliated strip, ct = cephalic tentacle, f = foot, hbgl = hypobranchial gland, mae = mantle edge, ol = oral lobe, p = propodium pe = penis, sn = snout).

mantle, however, occasionally emitted from the left side, a result of cilia that covers left mantle edge laterally and extend one fourth of the way across anterior mantle edge (Fig. 12). Majority of exudate is moved out of the right side of mantle cavity by ciliated strips. Pigmented hypobranchial gland shape is variable, comprised of large cells filled with thick yellow-white contents (released when snail is disturbed). Pigmented hypobranchial gland divided into partitions, with cells forming an oblong organ having one or several salient projections (Figs. 7, 11). Projections arranged generally perpendicular to the long axis of the gland. Perimeter of hypobranchial gland may be open (not continuous) or entirely closed. Ventral and dorsal ciliated strips (right side of mantle cavity) join posteriorly but extend only a short distance into mantle cavity (Fig. 12). Water flow is from left to right. Large pallial heart, with contractions at about 80/min. No pallial kidney was found. Rectum-anus on right side, near posterior end of mantle cavity.

Reproductive system (Figs. 9, 10, 12): Simultaneous hermaphrodite. Pallial portion of reproductive tract consists of both male and female counterparts. Penis on right side of mantle floor on snail's neck (Figs. 9, 12). Penis attenuated anteriorly, with bulbous posterior and scattered cilia (Fig. 10). Vas deferens joins bulbous por-

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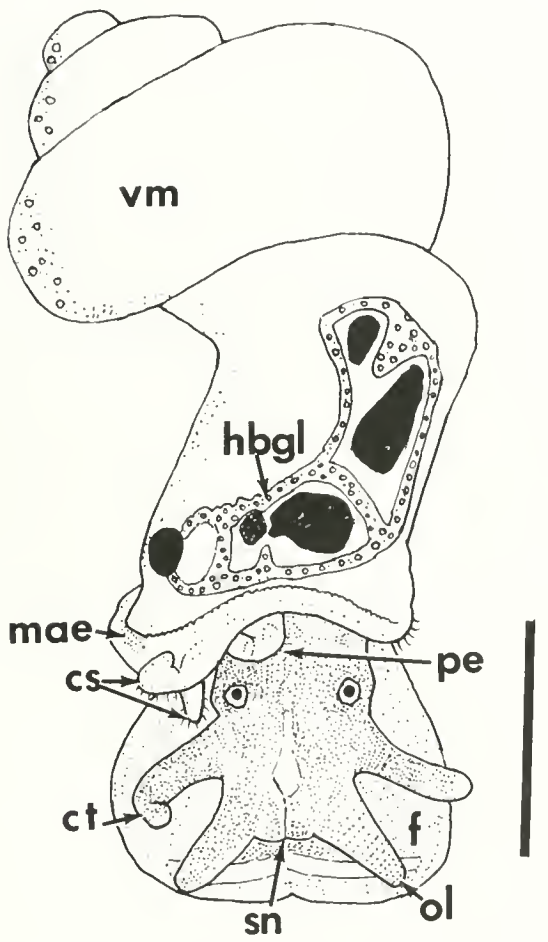

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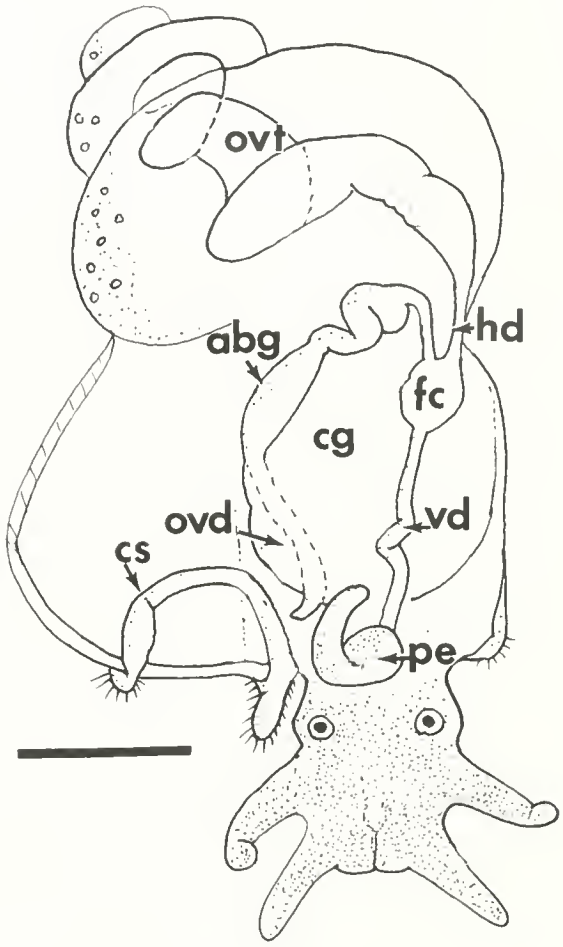


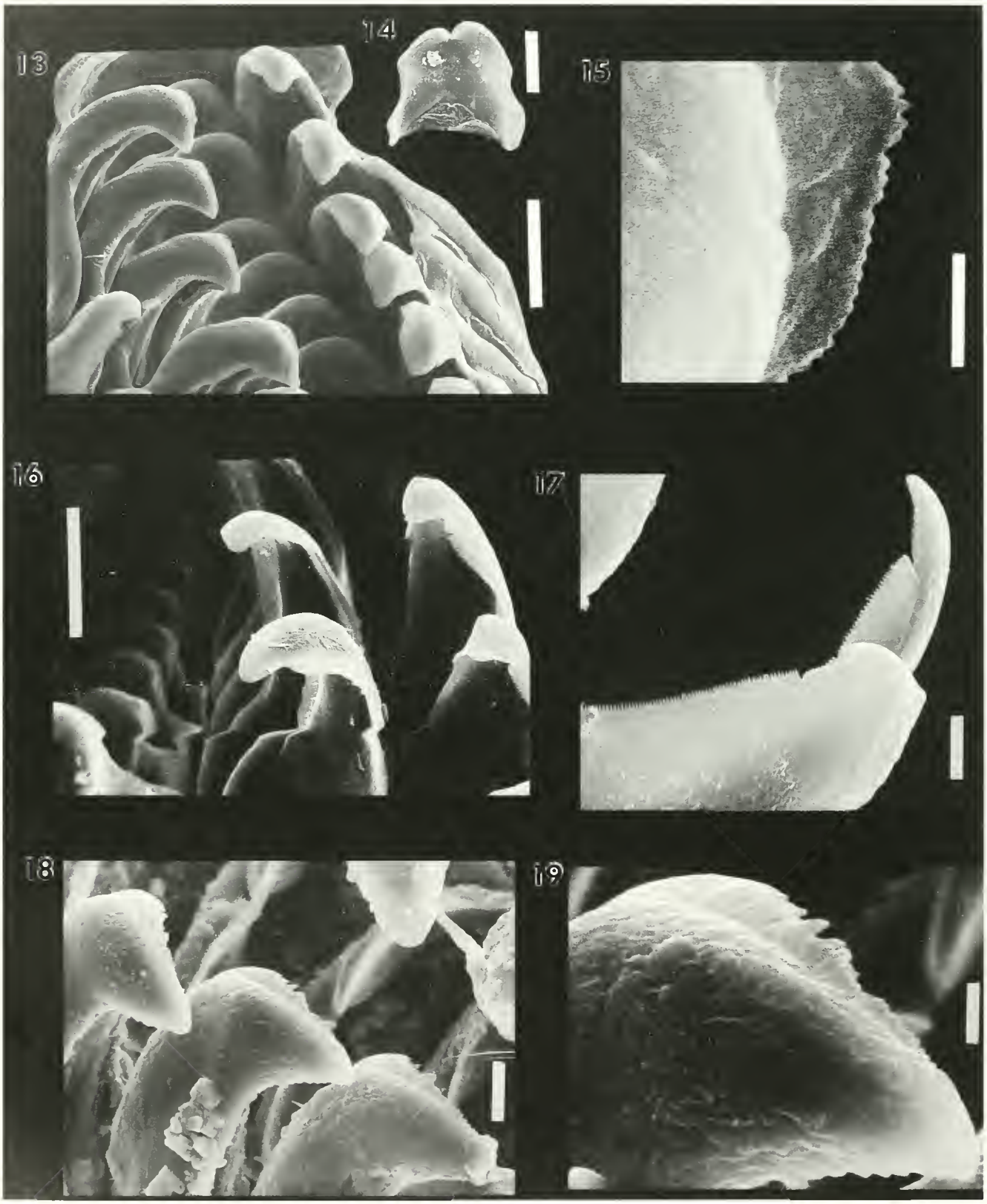
Figures 11–12. Diagrams of the anatomy of *Rissoella caribaea*. **11.** External anatomy of *R. caribaea* (scale bar = 250 μm). **12.** Mantle cavity and reproductive tract of *R. caribaea* (scale bar = 250 μm). (abg = albumen, cg = capsule gland, cs = ciliated strip, ct = cephalic tentacle, fc = fertilization chamber, hbgl = hypobranchial gland, hd = hermaphroditic duct, mae = mantle edge, ol = oral lobe, ovd = oviduct, ovt = ovotestis, pe = penis, sn = snout, vd = vas deferens, vm = visceral mass).

tion, extends posteriorly through mantle floor to fertilization chamber. Fertilization chamber joins hermaphroditic duct that extends posteriorly to join ovotestis within visceral mass (Fig. 12). Hermaphroditic duct serves as a conduit for eggs and sperm and possibly as seminal vesicle, as endogenous sperm are often present. Ovotestis coils within visceral mass on columellar side. Oviduct travels posteriorly from fertilization chamber turns and extends anteriorly, becoming part of capsule gland. Female duct terminates as a short papilla on the mantle floor, immediately posterior and on the right side of penis (Fig. 12). Double-layered egg capsule typically contains two embryos. Larval development unknown.

DISCUSSION

Rissoella caribaea was first described by Rehder (1943a), who stated that "It lives in sparsely populated colonies on clean rocks, actively moving about, its white tentacles contrasting strongly with the black body, which is visible through the almost transparent shell." Later Robertson (1961a) described the operculum, radula, and external morphology of *R. caribaea*. He determined that the shell and radula of *R. caribaea* (type species of the subgenus *Phycodrosus* Rehder, 1943) closely resembles that of *R. zebra* (type species of the subgenus *Jeffreysilla* Thiele, 1925). The difference he noted were that the rachidian of *R. caribaea* is more narrow, with "untoothed cusps". On the basis of his comparison of these two species, he determined that the subgenus *Phycodrosus* is a junior synonym of *Jeffreysilla*.

When the anatomy of *R. caribaea* (this study) is compared to the other rissoellid species for which the internal anatomy is known, there are a number of similarities and differences (Fretter, 1948; Simone, 1995). In 1948,



Figures 13–19. Scanning electron microphotographs of the radula of *Rissoella caribaea*. **13.** Radular ribbon, each row consisting of a rachidian, and a single lateral and marginal tooth on each side (scale bar = 10 μm). **14.** Rachidian tooth (scale bar = 10 μm).

Fretter described the biology and anatomy of two rissoellids (*Rissoella diaphana* and *R. opalina*) inhabiting the coralline tidepools of the British Isles. She determined that although their internal anatomy is similar, the two species are easily distinguished by shell shape, tentacles, and snout morphology. As in the rissoellids described by Fretter (1948), *Rissoella caribaea* exhibits intraspecific variation in the amount of pigmentation and color of the exposed body parts (= headfoot) and visceral mass, which is visible through the transparent shell. All rissoellids have a pair of cephalic tentacles and a pair of oral or triangular lobes that Fretter (1948) and Simone (1995) described as bifurcations of the snout. The oral lobes (Figs. 7, 11) of *Rissoella caribaea* are separate from the bifid snout, as illustrated by Ponder and Yoo (1977) for *R.* (*Rissoella*) *atrimacula* from S.W. Australia. In most species, the oral lobes are shorter and slightly wider than the tentacles. Rissoellids have well developed black eyes, containing large lenses. The eyes are posterior to the tentacles and high on the head, atop a slight protuberance, that in *R. caribaea* is surrounded by an area of unpigmented tissue (Fig. 11). Simone described the eyes as being on short stalks, however his illustrations of *Rissoella ornata* show the eyes to be on similar, slight protuberances, and not stalks.

The pedal gland of *R. caribaea* produces an attachment thread, which it uses to secure itself to the surrounding substratum. No attachment thread was observed in *R. diaphana* or *R. opalina*. However, the pedal gland produces a secretion, probably mucus, which is "essential to the locomotor mechanism of the snail" (Fretter, 1948; Fretter & Graham, 1962). In *R. ornata*, as in other taxa, the pedal mucous gland opening is located in a medial, longitudinal slit in the posterior half of the foot's ventral surface. No attachment thread or mucus production was reported for *R. ornata*, because no living snails were available to Simone (1995).

The mantle cavity of rissoellids is reduced in size by the large capsule gland and duct that projects dorsally from the body wall. As in the two species described by Fretter (1948) neither a gill nor an osphradium is present in *R. caribaea*. Simone (1995), however, reported the presence of "gill vestiges," with functional cilia and variable leaflet number and shape in *R. ornata*. These gill vestiges are located on the left side of the mantle roof, just posterior of anterior mantle edge. As in *R. opalina* and *R. diphana* the rectum-anus of *R. caribaea* is located on right posterior portion of the mantle floor. However, unlike *R. caribaea*, the two British taxa have two rows of ciliated strips extending anteriorly from each side of rectum; one on the roof and one on the floor of the mantle cavity. In *R. caribaea*, both ventral and dorsal ciliated strips extend only a short distance into the mantle cavity where they join (Fig. 12). Furthermore, in *R. opalina* and *R. diaphana* underlying each ciliated strip is a broad band comprised of secretory cells. In particular, the dorsal band is broader and composed entirely of mucous cells, which Fretter (1948) suggested may function as the hypobranchial gland. No bands of mucus producing cells were observed within the ciliated strips of *R. caribaea*. Dissimilarly, the rectum/anus of *R. ornata* apparently extends along the right side of the mantle cavity to terminate in what Simone (1995) described as a special fecal chamber. This chamber is located at the right corner of the mantle edge. From his illustrations it appears that Simone (1995:figs. 9, 10) confused the ventral and dorsal ciliated strips (similar to those in *R. caribaea*), with what he respectively defined as head flap, and folds, both perpendicular and parallel to the mantle border. The hypobranchial gland of *R. ornata*, located posterior to these structures within the mantle roof is not present in *R. caribaea*. Although no kidney was found in *R. caribaea*, it is present within the mantle cavity in both *R. opalina* and *R. diaphana*, opening near the anus (Fretter, 1948; Fretter & Graham, 1962). In *R. ornata*, the kidney is between stomach and albumen gland within the visceral mass (Simone, 1995).

The alimentary tract of *R. caribaea* extends posteriorly from its bifid snout to the jaw and then the radula (Fig. 13). The jaw of *R. caribaea* is very similar to the jaw of *R. ornata* (Simone, 1995). The radulae of *R. opalina* and *R. diaphana* (not figured) are similar to that *of R. caribaea*. However, Fretter (1948) stated that the lateral and marginal teeth are absent and replaced by intermediate teeth. The radula of *R. ornata* is short (10–12 rows), each row containing a single rachidian, with approximately 10 equal sized cusps and one pair each of cuspidate lateral and marginal teeth. Esophagus, stomach, digestive gland and intestine-anus are quite similar for these taxa, the only difference being the position of the rectum-anus (see above).

Rissoellids are hermaphrodites, simultaneously producing both eggs and sperm, within the same tubules of the ovotestis, although Fretter (1948) reported that sperm may mature first. The gonadal duct (= hermaphrodite duct, Fretter, 1948; Fretter & Graham, 1962; Simone, 1995) or hermaphroditic duct (this study) extends anteriorly from the gonad to join the fertilization chamber in *R. caribaea* (Fig. 12). In contrast, the hermaphrodite duct in *R. ornata*, *R. opalina*, and *R. diaphana* splits into a vas deferens and an albumen gland. The vas deferens passes anteriorly beneath the pallial oviduct, to the left of the middle of the mantle floor. That portion of the vas deferens just prior to the duct's terminus is the glandular prostrate. The hermaphroditic duct appears to function as the seminal vesicle in *R. caribaea*

←

15. Enlargement of rachidian cutting edge, top portion (scale bar = 1μm) **16.** Lateral and marginal teeth (scale bar = 10 μm). **17.** Fine serrations on sides of lateral and marginal teeth (scale bar = 2 μm). **18.** Crested marginal teeth (scale bar = 2 μm). **19.** Enlargement of single marginal crest (scale bar = 1 μm).

and in the species described by Fretter (1948). Fretter (1948) described a deep gutter, on the median side of the ventral longitudinal strip, into which the female duct opens "at summit of long papilla." At the anterior part of the female duct terminus is the folded penis sitting in a groove, with its tip immediately anterior to the female aperture. Fretter and Graham (1962) also described a third conduit that comprises a muscular sac connected to the posterior end of the capsule gland by a short duct and opens to the mantle cavity via a longer duct. They suggested that it removes excess "secretions and sperm" from the genital duct and is homologous with a receptaculum seminis. In *R. caribaea,* the penis is on the right side of the mantle floor on snail's neck (Figs. 9,10) and not within a groove. The reproductive tract in *R. ornata* is similar to that in *R. opalina,* however its vas deferens extends anteriorly on the right side of the head and ends as a short tubular penis. The albumen and capsule glands of *R. ornata* are very similar to those present in *R. caribaea, R. diaphana,* and *R. opalina.*

Although this study provides new insights into rissoellid biology, and more specifically the anatomy of *Rissoella caribaea,* it is not possible (due to limited available data) to assess its systematic position within the family. As determined by Robertson (1961a), *Rissoella caribaea* possesses the following characters typical of the family: 1) oral lobes, 2) perpendicular opercular peg, 3) large hypobranchial gland (=PMO? *sensu* Robertson, 1985; Wise, 1996), and 4) symmetrical radula consisting of a single central tooth and one pair each of comb-shaped lateral and marginal teeth. However, these features are present in all known rissoellids and cannot be used to resolve relationships within the rissoellids. Moreover, studies utilizing radular morphology to separate rissoellid species into subgenera have seldom examined enough specimens or species to reach well-supported conclusions. Geographical variation within a species, ontogenetic changes, and whether or not tooth morphology is a result of diet or phylogeny remain areas that are underexplored for rissoellids. Until a better understanding of known rissoellid taxa exists, relationships within the genus or family cannot be robustly resolved.

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The Molluscan Fauna of the Wawa River Region, Miskito Coast, Nicaragua: Ecology, Biogeographical Implications, and Descriptions of New Taxa

Edward J. Petuch
Department of Geology
Florida Atlantic University
Boca Raton, Florida 33431 USA
and
Department of Paleontology
The Graves Museum of Archaeology
and Natural History
Dania, Florida 33004 USA

ABSTRACT

Faunal surveys (1991–1992) of the biologically-unexplored Wawa River region of the Miskito Coast of Nicaragua have shown that the intertidal and estuarine areas contain four distinct molluscan assemblages; the *Neritina—Polymesoda* Assemblage, the *Littorina—Petricola* Assemblage, the *Agaronia-Micromactra* Assemblage, and the *Hastula—Donax* Assemblage, and that the shallow subtidal area contains a single assemblage, the *Ficus-Pacipecten* Assemblage. A list of macromollusks found in these five assemblages is given, and eight new endemic mollusks are described. These include: (Gastropods) *Ficus villai* n.sp. (Ficidae), *Cancellaria mediamericana* n.sp. (Cancellariidae), *Conus paschalli* n.sp. (Conidae), and (Bivalves) *Noetia* (s.s.) *lindae* n.sp. (Arcidae), *Plicatula miskito* n.sp. (Plicatulidae), *Mactra inceri* n.sp., *Micromactra miskito* n.sp. (both Mactridae), and *Petricola (Petricolaria) donnae* n.sp. (Petricolidae). This new faunal data, in conjunction with previous Central American biogeographical studies, has demonstrated the existence of a new molluscan faunal area within the western Caribbean, here referred to as "Miskitia". The Miskitian area, which may represent a new subprovince of the Caribbean Molluscan Province, is distinctly Panamic-appearing, containing molluscan assemblages that are dominated by normally-Eastern Pacific genera such as *Agaronia*, *Noetia* (s.s.), *Pacipecten*, and *Micromactra*

INTRODUCTION

Within the past decade, faunal surveys in previously-unexplored areas of the Caribbean Sea region have uncovered large numbers of new and unusual marine mollusks (Petuch, 1987, 1988, 1990). Besides underscoring our lack of knowledge of such geographically-proximate malacofaunas, these discoveries have shown that the Caribbean is not faunally homogeneous as was previously thought (Warmke & Abbott, 1961), but is composed of at least seven discrete, mutually-exclusive subregions (Petuch, 1981,1982,1987,1988, 1997). Each of these subregions has been found to contain a high degree of endemism at both the generic and specific level and, altogether, have demonstrated that the geographically-small Caribbean Sea region contains the highest level of molluscan diversity found in the Americas.

While the coastal faunas of the Yucatan Peninsula, Honduras (Petuch, 1981,1987,1988; Vokes & Vokes, 1983), Costa Rica (Houbrick, 1968), and Panama (Olsson & McGinty, 1958; Petuch, 1990; Radwin, 1969) have been studied, the mollusks of the Caribbean coast of Nicaragua had never been adequately surveyed and the region has remained enigmatic. Over the past ninety years, only a few scattered reports on Caribbean Nicaraguan mollusks have appeared in the literature (reviewed in next section), and these have only offered tantalizing bits of information that hinted at a very unusual and highly endemic fauna. In December, 1991 and July, 1992, while working with the Caribbean Conservation Corporation of Gainesville, Florida (under the auspices of IRENA (Instituto de Recursos Naturales), the environmental agency of the Nicaraguan government), I had the opportunity to visit and collect along a part of the Miskito Coast near the mouth of the Wawa River. This study, coincidentally conducted in the only area of the entire coast that had ever been sampled (Fluck, 1905a, 1905b, 1905c, 1905d, 1905e, 1906; see next section), is part of a major biotic survey that is being undertaken by the Nicaraguan government in preparation of the establishment of a wildlife and cultural protected zone along the Miskito Coast.

The Miskito Coast was found to contain a highly unusual molluscan fauna, one that was both atypical of the Caribbean Molluscan Province and that exhibited a high degree of endemism. In many ways, the Nicaraguan Caribbean coastal malacofauna more closely resembles the faunas of the Eastern Pacific Panamic Province and the eastern South American Brazilian Province than it does

the fauna of the surrounding Caribbean Province. This Panamic-Brazilian appearance was further emphasized by the discovery of new endemic species, several of which belong to genera that were thought to have been restricted to the Panamic and Brazilian Provinces.

In this paper, descriptions of the various coastal environments of the Wawa River area are given, along with lists of the dominant macromollusks found in each habitat. Eight new Miskito Coast species are described, including: Gastropods—*Ficus villai* n.sp. (Ficidae), *Cancellaria mediamericana* n.sp. (Cancellariidae), *Conus paschalli* n.sp. (Conidae); Bivalves—*Noetia lindae* n.sp. (Arcidae), *Plicatula miskito* n.sp. (Plicatulidae), *Mactra inceri* n.sp., *Micromactra miskito* n.sp. (both Mactridae), and *Petricola (Petricolaria) donnae* n.sp. (Petricolidae). A discussion of the biogeographical relationships of the Miskito Coast fauna is given in the final section.

Previous Malacological Research Along The Miskito Coast Of Nicaragua

Prior to the present research, only one other attempt at a comprehensive survey of the macromollusks of the Miskito Coast had ever been undertaken. This pioneer work was done by the Rev. W.H. Fluck, a Moravian missionary who ministered to the Miskito and Sumo Indians at the turn of the century. In a series of six papers published in 1905 and 1906, Fluck gave interesting anecdotal insights into the environments and natural history of the area, molluscan food utilization by the local Indians, and detailed descriptions of some of his techniques for collecting mollusks. Most importantly, he provided several annotated species lists, arranged phylogenetically, of the gastropods and bivalves that had been collected near the mouth of the Wawa River, Wounta and Bluefields Lagoons, and the offshore Man-of-War and King's Keys.

In four of his papers, Fluck lists fifty-two species of marine and estuarine mollusks from the Wawa River area, one of which he described as new (*Strombus pugilis nicaraguensis* Fluck, 1905). Of these, five were not encountered in the present study; the gastropods *Tonna maculosa, Polinices lacteus, Cymatium pileare*, and *Columbella mercatoria*, and the bivalve *Arcopagia fausta*. Here, arranged by publication date, are lists of Fluck's Wawa species, along with their updated taxonomic designations (where applicable);

Fluck, 1905b. (*Shell Collecting on the Mosquito Coast of Nicaragua—II.* The Nautilus 19(2):16–19).

Fluck's Taxon	Updated Nomenclature
Murex brevifrons Lamarck	*Chicoreus mergus* E. Vokes
Murex bellus Reeve	*Vokesimurex garciai* (Petuch)
Cymatium pileare Lamarck	
Purpura floridana Conrad	*Thais floridana* (Conrad)
Fasciolaria tulipa Linnaeus	
Melongena melongena Linnaeus	
Nassa vibex Say	*Nassarius vibex* (Say)
Voluta virescens Solander	*Voluta lacertina* Petuch
Marginella apicina Menke	*Prunum pruinosum* (Hinds)
Marginella guttata Dillwyn	*Prunum guttatum* (Dillwyn)
Oliva(Agaronia) testacea Lam.	*Agaronia hilli* Petuch
Columbella mercatoria Linnaeus	
Columbella (Anachis) lyrata Sow	*Costanachis veleda* (Duclos)
Cancellaria reticulata Linnaeus	*Cancellaria mediamericana* n.sp.
Terebra cinerea Gmelin	*Hastula cinerea* (Born)

Fluck, 1905d (*Shell Collecting on the Mosquito Coast of Nicaragua*—IV. The Nautilus 19(5):55–57).

Fluck's Taxon	Updated Nomenclature
Cypraea exanthema Linneaus	*Cypraea zebra* Linnaeus
Dolium perdix Linnaeus	*Tonna maculosa* Linnaeus
Pyrula papyratia Say	*Ficus villai* n.sp.
Polinices brunnea Link	*Polinices hepaticus* (Röding)
Polinices lacteus Guilding	
Crepidula convexa Say	
Vermicularia spirata Philippi	
Litorina lineata Philippi	*Littorina lineata* d'Orbigny
Litorina columellaris D'Orb.	*Littorina nebulosa* (Lamarck)
Litorina angulifera Lam.	*Littorina angulifera* (Lamarck)
Neritina lineata var. *reticulata*	*Neritina piratica* Russell, 1940

Fluck, 1905e. (*Shell Collecting on the Mosquito Coast of Nicaragua-V.* The Nautilus 19(7):78–80).

Fluck's Taxon	Updated Nomenclature
Pholas campechiensis Gmelin	
Tagelus pocyii Dall	*Tagelus plebeius* (Lightfoot)
Periploma inequivalvis Schum.	*Periploma margaritaceum* (Lamarck)
Mactra(Mactrella) alata Spengler	*Mactrellona alata* (Spengler)
Mulinia guadeloupensis Recluz	*Mulinia cleryana* (Orbigny)

Fluck, 1906. (*Shell Collecting on the Mosquito Coast of Nicaragua-VI.* The Nautilus 20(1):1–4).

Fluck's Taxon	Updated Nomenclature
Tellina (Eurytellina) angulosa Gmelin	
Tellina (Cyclotellina) fausta Pulteney	*Arcopagia fausta* (Pulteney)
Sanguinolaria (Psammotella) operculata(Gmelin)	*Sanquinolaria cruenta* (Lightfoot)
Strigilla carnaria Linnaeus	
Iphigenia brasiliana (Lamarck)	
Donax denticulatus Linnaeus	
Donax cayennensis Lamarck	*Donax striatus* Linnaeus
Pitar (Hysteroconcha) dione (Linnaeus)	
Chione cancellata (Linnaeus)	
Cyrena (Polymesoda) panamensis Prime	*Polymesoda placans (Hanley)*

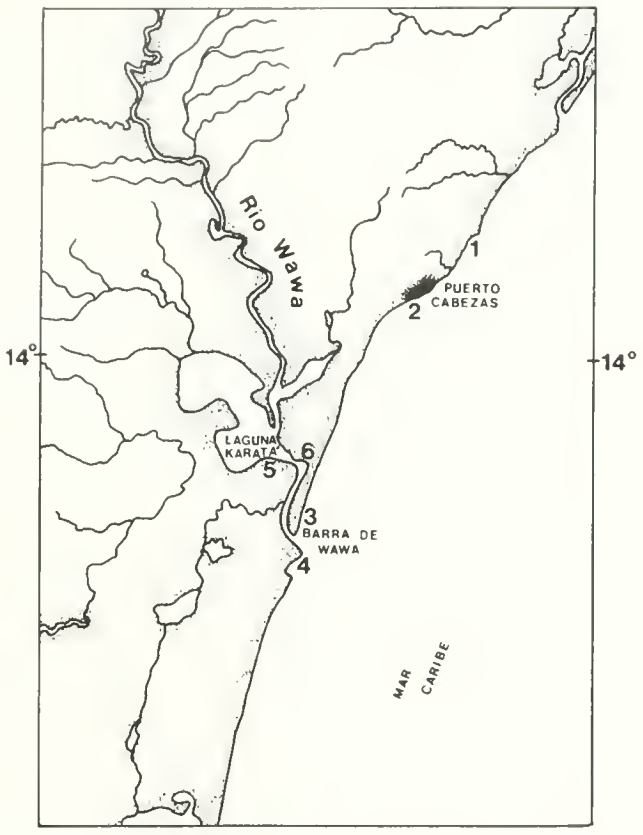


Figure 1. Map of the Miskito Coast of Nicaragua, in the vicinity of the Wawa River mouth, showing collection stations. Distance between Stations 1 and 4 is approximately 11 km. 1 = shallow embayment on southern side of Bragman's Bluff (containing *Agaronia—Micromactra* Assemblage); 2 = clay cliffs and clay talus "reefs" immediately north and south of Puerto Cabezas (containing *Littorina—Petricola* Assemblage); 3 = beach on outer side of Barra de Wawa, northern side of Wawa River mouth (containing *Hastula—Donax* and *Ficus—Pacipecten* Assemblages); 4 = beach on southern side of Wawa River mouth, adjacent to Wawa Village (containing *Hastula—Donax* and *Ficus—Pacipecten* Assemblages); 5 = southern shore of Laguna Karatá, at Karatá Village (containing *Neritina—Polymesoda* Assemblage); 6 = mangrove jungle at Salonque de Kauropura (containing *Neritina—Polymesoda* Assemblage).

Tivela mactroides (Born)	
Chama congregata Conrad	
Arca umbonata Lamarck	*Arca imbricata* Bruguière
Scapharca incongrua var. *brasiliana* Lam.	*Anadara brasiliana* (Lamarck)
Arca occidentalis Philippi	*Arca zebra* (Swainson)
Pinna muricata Linnaeus	*Atrina seminuda* (Lamarck)
Pecten dislocatus Say	*Pacipecten leucophaeus* (Reeve)
Ostrea virginica Gmelin	*Crassostrea virginica* (Gmelin)

Since Fluck's series of papers, only a few scattered references to the Miskito Coast fauna have appeared in the Caribbean molluscan literature. Most of these have been in the *Johnsonia* series of monographs published at Harvard University (1941–1974)(ie. Clench & Abbott, 1941; Bequaert, 1942, *etc.*), and were based upon the Fluck Collection in the Museum of Comparative Zoology. No references to newly-collected Miskito material have been mentioned prior to the present study.

In the 1980's, I had received several suites of unusual western Caribbean gastropods from local commercial shell dealers, particularly Mr. Leonard C. Hill of Miami, Florida. Within these specimen lots were large numbers of new species that had been dredged from shallow depths (10–35m) off Roatan Island and the northern Honduras coast by commercial shrimp boats. Many of these were subsequently described by myself (Petuch, 1987) and were later discussed within a geochronological and biogeographical framework (Petuch, 1988:149–156). Although the bulk of these new taxa were from the area immediately north of the Miskito Coast, a few have now been collected in Nicaragua and have been found to be ecologically-dominant Miskito organisms. Two of these recently described gastropods, which range from the Roatan Island-Punta Patuca area of Honduras to the Nicaraguan Miskito Coast, include *Agaronia hilli* Petuch, 1987 and *Vokesimurex garciai* (Petuch, 1987).

Following the legacy of the Rev. Fluck and his pioneer research, I here report on the most recent malacological survey of the Miskito Coast. In total, one hundred and four species, from five distinct molluscan assemblages, were collected, doubling Fluck's total of fifty-two species. Of these, eight are new to science. The habitats and ecological preferences of the molluscan assemblages of the Wawa River area of the Miskito Coast are given in the following section.

Collecting Stations And Coastal Environments

In order to gain a general insight into the molluscan faunas of the varied coastal habitats, six widely-spaced collecting sites were selected in the Puerto Cabezas-Wawa River area (Figure 1). Four of these were along the open coast, ranging from approximately 2.5 km north of the main pier of Puerto Cabezas southward to the southern shore of the Wawa River mouth. Two others were from within the estuary of the Wawa River. From these six sites, altogether, five distinct molluscan assemblages could be discerned. The assemblages are named after dominant or characteristic gastropods and bivalves, one of each, and these include: *1.* The *Neritina—Polymesoda* Assemblage (brackish water, estuarine), 2. the *Littorina—Petricola* Assemblage (coastal clay cliffs), 3. the *Agaronia—Micromactra* Assemblage (protected coastal, quiet intertidal), *4.* the *Hastula—Donax* Assemblage (open coastal, high energy intertidal), and 5. the *Ficus—Pacipecten* Assemblage (offshore, shallow subtidal). The physical environment and molluscan assemblages of each collecting site are discussed herein.

Station 1. (*Agaronia—Micromactra* Assemblage)

An unnamed, widely open embayment containing shallow, relatively quiet water conditions, was located at ap-

proximately 2.5 km north of Puerto Cabezas, between the mouth of La Bocana Creek and Bragman's Bluff. The southward curvature of Bragman's Bluff, along with its accompanying sandstone and clay block talus reef, both offer protection from strong easterly and northeasterly winds and waves, allowing the creation of almost lagoonal conditions within the open embayment. These quiet conditions, which are especially prevalent immediately south of the bluff, are further enhanced by the presence of a large sand bar that runs parallel to the coast just offshore.

This shallow (0–1m depth) environment, comprising a flat muddy-sand substrate and murky water conditions with only minimal wave action, contained a highly unusual, highly atypical Caribbean molluscan assemblage. The dominant mollusks, found nowhere else in the Caribbean province, give this assemblage a distinctive Eastern Pacific appearance, and the entire community closely resembles assemblages that are found on similar biotopes along western Central America. Characteristic mollusks from the Bragman's Bluff open embayment locality include:

Gastropods

Strombus pugilis nicaraguensis Fluck, 1905 (Figure 6)
Agaronia hilli Petuch, 1987 (Figures 4, 5)
Conus paschalli n.sp. (Figures 2,3)

Bivalves

Noetia lindae n.sp. (Figures 9, 10)
Plicatula miskito n.sp. (Figures 16–19)
Diplodonta notata (Dall & Simpson, 1901)
Trachycardium muricatum (Linnaeus, 1758)
Mactra inceri n.sp. (Figures 7, 8, 11)
Micromactra miskito n. sp. (Figures 12, 13)
Mulinia cleryana (Orbigny, 1846) (Figure 20)
Macoma brevifrons (Say, 1834)
Macoma constricta (Bruguière, 1792)
Tellina punicea Born, 1778
Sanguinolaria sanguinolenta (Gmelin, 1791)
Periploma margaritaceum (Lamarck, 1801) (Figure 21)

Similar biotopes from around the Caribbean Basin all contain assemblages that are typically dominated by olivid gastropods of the genera *Oliva* (particularly members of the *Oliva reticularis* Lamarck, 1811 species complex; see Petuch & Sargent, 1986:120–122) and *Olivella*, and bivalves of the genera *Glycymeris*, *Divaricella*, *Codakia*, *Anomalocardia*, and the tellinids *Tellina radiata* Linnaeus, 1758 and *Tellina listeri* Röding, 1798. All of these taxa were missing from the Bragman's Bluff collecting station and were not found at any other Miskito coast locality (both this study and that of the Rev. Fluck in 1905–1906). Instead, the gastropod component at Bragman's Bluff was dominated by the olivid genus *Agaronia* and the bivalve component by mactrids (*Mactra*, *Micromactra*, and *Mulinia*). The primarily-Panamic genus *Micromactra* (represented by *M.miskito* n.sp.), previously unknown in the Caribbean Province, was especially common at Station 1.

Behind the sand bar, directly off the beach south of Bragman's Bluff, large beds of dead bivalve shells have accumulated. These beds, composed mostly of dead *Noetia* valves, produce the proper substrate for the attachment of the dwarf oyster, *Plicatula miskito* n.sp.. This new species, which closely resembles the Eastern Pacific *Plicatula penicillata* Carpenter, 1857, further demonstrates the Panamic appearance of the Bragman's Bluff assemblage.

Station 2. (*Littorina—Petricola* Assemblage)

From the main pier of Puerto Cabezas northward to the mouth of Laguna Krukira (approximately 8 km north), the coast is characterized by high (20–50m) red and white clay cliffs (Figure 14). Lenses of rounded quartzite pebbles are plentiful within the cliffs and, upon erosion, often form thick pebble beds at the cliff bases. At several localities immediately north of the pier, and particularly adjacent to the mouth of La Bocana Creek, large talus slopes composed of massive blocks of clay and soft sandstone have extended seaward and have, in effect, produced "rocky" intertidal environments. These clay "reefs" often extend into the subtidal region and offer a wide variety of habitats within the vertical range. The clay cliffs biotope at, and immediately northward of Puerto Cabezas, was chosen as the second collection station.

The intertidal-shallow subtidal clay cliff and clay "reef" environment contained a very impoverished molluscan fauna, with only a few species dominating the area. Characteristic mollusks from the Puerto Cabezas clay cliffs locality include:

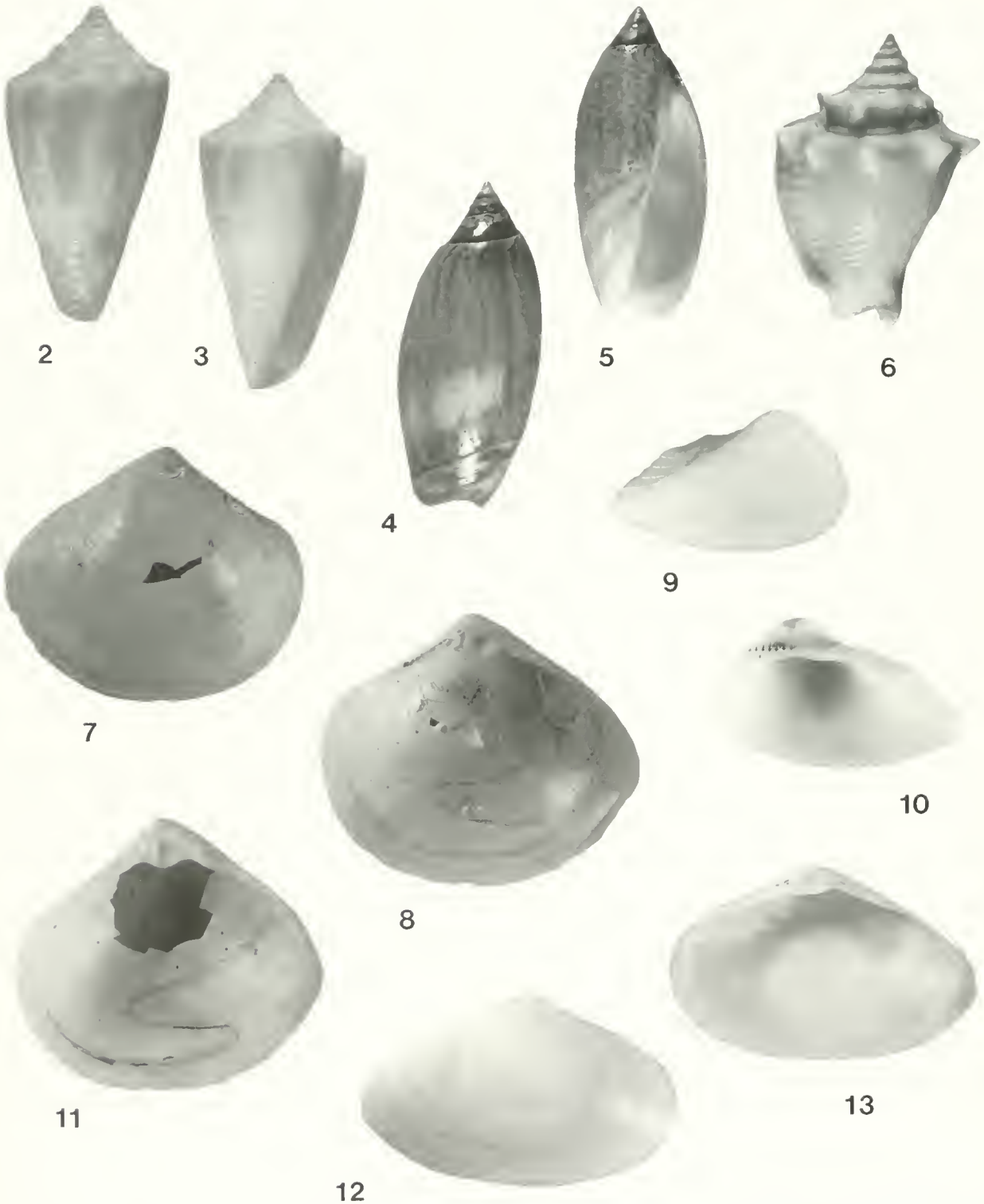
Gastropods

Diodora cayenensis (Lamarck, 1822)
Littorina lineata Orbigny, 1842
Littorina nebulosa (Lamarck, 1822)
Littorina riisei Mörch, 1876
Thais floridana (Conrad, 1837)

Bivalves

Pholas campechiensis Gmelin, 1791
Petricola (Petricolaria) donnae n.sp. (Figures 24, 25)

What was particularly impressive about the clay cliffs fauna was the noticeable absence of typical common Caribbean hard substrate taxa, many of which were expected to have been encountered along this coast. Absent from the supratidal zone were the classically Caribbean littorinid genera *Tectarius (Cenchritis)*, *Nodilittorina (Echinolittorina)* and *Echininus*. Within the intertidal zone, the absence of the neritid genera *Linnerita*, *Theliostyla*, and *Puperita*, the potamidid genus *Batillaria*, the cerithiid genus *Cerithium (Thericium)*, and the pulmonate genus *Siphonaria* was particularly



Figures 2–13. Mollusks characteristic of the *Agaronia—Micromactra* Assemblage. **2, 3.** *Conus (Leptoconus) paschalli* new species, holotype, length 26 mm; **4, 5.** *Agaronia hilli* Petuch, 1987, length 39 mm; **6.** *Strombus pugilis nicaraguensis* Fluck, 1905, length 58 mm; **7, 8.** *Mactra inceri* new species, holotype, length 35.5 mm; **9, 10** *Noetia* (s.s.) *lindae* new species, holotype, length 25.5 mm; **11.** *Mactra inceri* new species, paratype, length 34 mm (pallial line outlined with ink); **12, 13.** *Micromactra miskito* new species, holotype length 30 mm.

Figure 14. Aerial view of clay cliff coastline in the vicinity of Puerto Cabezas. Arrows point to clay talus "reefs" near the mouth of La Bocana Creek, on the northern side of the city. Station 2 included these cliffs and "reefs" and others immediately to the south (to the left). The holotype of *Petricola (Petricolaria) donnae* n.sp. was collected on the beach between the first two arrows on the left.

noteworthy. Instead, the entire intertidal zone was dominated by only three species of *Littorina*, of which *Littorina nebulosa* (Lamarck, 1822) was the most abundant.

The shallow subtidal zone of the clay "reefs" exposed at extreme low tides, was relatively barren externally, but was riddled with immense numbers of holes. The holes represented the burrows of the pholadid and petricolid bivalves *Pholas campechiensis* Gmelin, 1791 and *Petricola (Petricolaria) donnae* n.sp., and these two burrowers were the dominant organisms in this area. The large carnivorous muricoidean gastropod *Thais floridana* (Conrad, 1837) was also frequently encountered on the subtidal clay "reefs", and several specimens were found to be feeding on the limpet *Diodora cayenensis* (Lamarck, 1822).

Stations 3 and 4. (*Hastula—Donax* Assemblage and *Ficus—Pacipecten* Assemblage).

South of the Puerto Cabezas pier, the high clay cliffs disappear, and the coastline becomes flattened with wide, jungle-lined beaches and high-energy surf zones. Along these beaches two distinct molluscan assemblages accumulate; a *Hastula-Donax*-dominated assemblage that lives in the sandy intertidal zone amid the heavy surf, and a *Pacipecten* dominated assemblage that lives in the subtidal area directly offshore (approximately 0.5 to 1 km off the coast, in depths of 10–25m). Most of the components of the former assemblage can be collected within the surf at low tide and their dead, beached shells are unusually well-preserved. The components of the latter assemblage, on the other hand, only wash up onto the beach after storms or heavy blows, and their shells are most always in a smashed, fragmentary condition. Preliminary information on the composition of Caribbean beach communities (ie. Warmke & Abbott, 1961: 17,19; Houbrick, 1968) and western Caribbean offshore communities (Radwin, 1969:229–236; Petuch, 1987:62–63; Petuch, 1990) made it possible to determine which of the two assemblages represented the home communities of all beach specimens collected.

The high-energy beach environment, the biotope of the *Hastula-Donax* Assemblage, houses the most typical Caribbean fauna found along the Miskito Coast. For study, two beach areas that particularly characterized this biotope were selected on either side of the Wawa River mouth; with Station 3 located on the northern side along the outer coast of the Barra de Wawa, and with

Figure 15. View of the beach along the southern side of the Wawa River mouth. Piles of driftwood, brought down by the strong river currents, line the beach for several kilometers. The Fig Shell, *Ficus villai* n.sp., and the scallop, *Pacipecten leucophaeus* (Reeve, 1852), were especially common along this area. Station 4 included this locality and the open beach environment in the distance. This is also the type locality of Fluck's *Strombus pugilis nicaraguensis* (which is plentiful as fresh beach specimens).

Station 4 located on the southern side adjacent to Wawa Village (Figure 15). Characteristic mollusks from the Wawa surf locality include:

Gastropods

Hastula cinerea (Born, 1778)

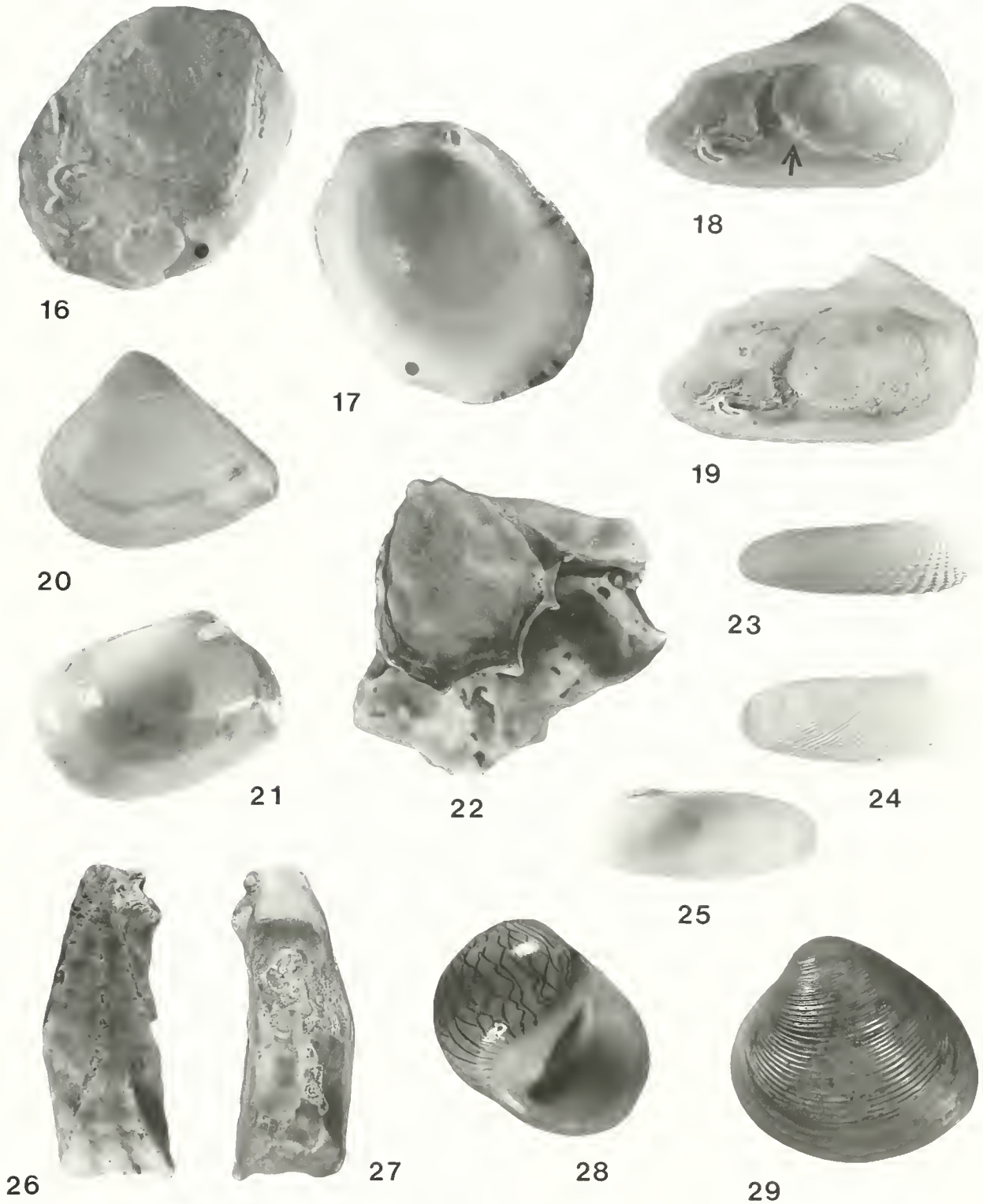
Bivalves

Solen obliquus Spengler, 1794
Strigilla carnaria (Linnaeus, 1758)
Strigilla gabbi Olsson and McGinty, 1958
Strigilla mirabilis (Philippi, 1841)
Strigilla pisiformis (Linnaeus, 1758)
Strigilla producta (Tryon, 1870)
Strigilla pseudocarnaria Boss, 1969
Tellina sybaritica Dall, 1881
Donax denticulatus Linnaeus, 1758
Donax mediamericanus Pilsbry, 1919 (Figure 43)
Donax striatus Linnaeus, 1767 (Figure 42)
Iphigenia brasiliana (Lamarck, 1818)
Tagelus plebeius (Lightfoot, 1786)
Pitar dione (Linnaeus, 1758)
Tivela mactroides (Born, 1778)

With the exception of *Donax mediamericanus* Pilsbry, 1919, which is endemic to the Caribbean coast of Central America (type locality, Livingston, Guatemala), all of the other members of this assemblage are wide-ranging tropical western Atlantic surf-loving species. Although the faunal composition of this assemblage is, by itself, unremarkable, the abundant presence of six sympatric species of the tellinid genus *Strigilla* and three species of large *Donax* is noteworthy. Other Caribbean surf eco-

→

Figure 16–29. Mollusks characteristic of the *Agaronia—Micromactra, Littorina—Petricola,* and *Neritina—Polymesoda* Assemblages. **16, 17.** *Plicatula miskito* new species, upper valve of holotype, length 13 mm; **18.** *Plicatula miskito* new species, interior view of bottom valve of holotype attached to interior of *Noetia lindae* valve. Arrow points to spondyloid hinge; **19.** *Plicatula miskito* new species, upper valve of holotype attached to bottom valve in life position, within *Noetia lindae* valve; **20.** *Mulinia cleryana*



(d'Orbigny, 1846), length 23 mm; **21.** *Periploma margaritaeeum* (Lamarck, 1801), interior of left valve, length 31 mm; **22.** *Crassostrea rhizophorae* (Guilding, 1828) upper specimen length 35 mm; **23.** *Petricola (Petricolaria) pholadiformis* (Lamarck, 1818), length 35 mm. From beach at Lake Worth, Florida, (for comparison with *Petricola donnae*); **24, 25.** *Petricola (Petricolaria) donnae* new species, holotype, length 28 mm; **26, 27.** *Crassostrea virginica* (Gmelin, 1791), length 97 mm. Elongated variant that resembles *Crassostrea labelleensis* Olsson & Harbison, 1953 from the Floridian Pleistocene; **28.** *Neritina piratica* Russel, 1940, length 13 mm; **29.** *Polymesoda placans* (Hanley, 1845), length 28 mm.

Figure 30. View of a section of the red mangrove (*Rhizophora mangle*) forest at Salonque de Kauropura, near Laguna Karatá. The arrow (extreme lower left center) points to a small clump of the mangrove oyster, *Crassostrea rhizophorae* (Guilding, 1828). The nerites *Neritina piratica* Russell, 1940 and *Neritina reclivata* (Say, 1822) were common here on submerged roots and oyster clumps. On the higher dry branches and roots, the periwinkles *Littorina nebulosa* (Lamarck, 1822) and *Littorina angulifera* (Lamarck, 1822) and the melampid *Melampus coffeus* (Linnaeus, 1758) could be found in abundance. Open muddy-sand bottom areas between mangrove forests housed large, dense colonies of the corbiculid bivalve *Polymesoda placans* (Hanley, 1845). This area encompassed Station 6.

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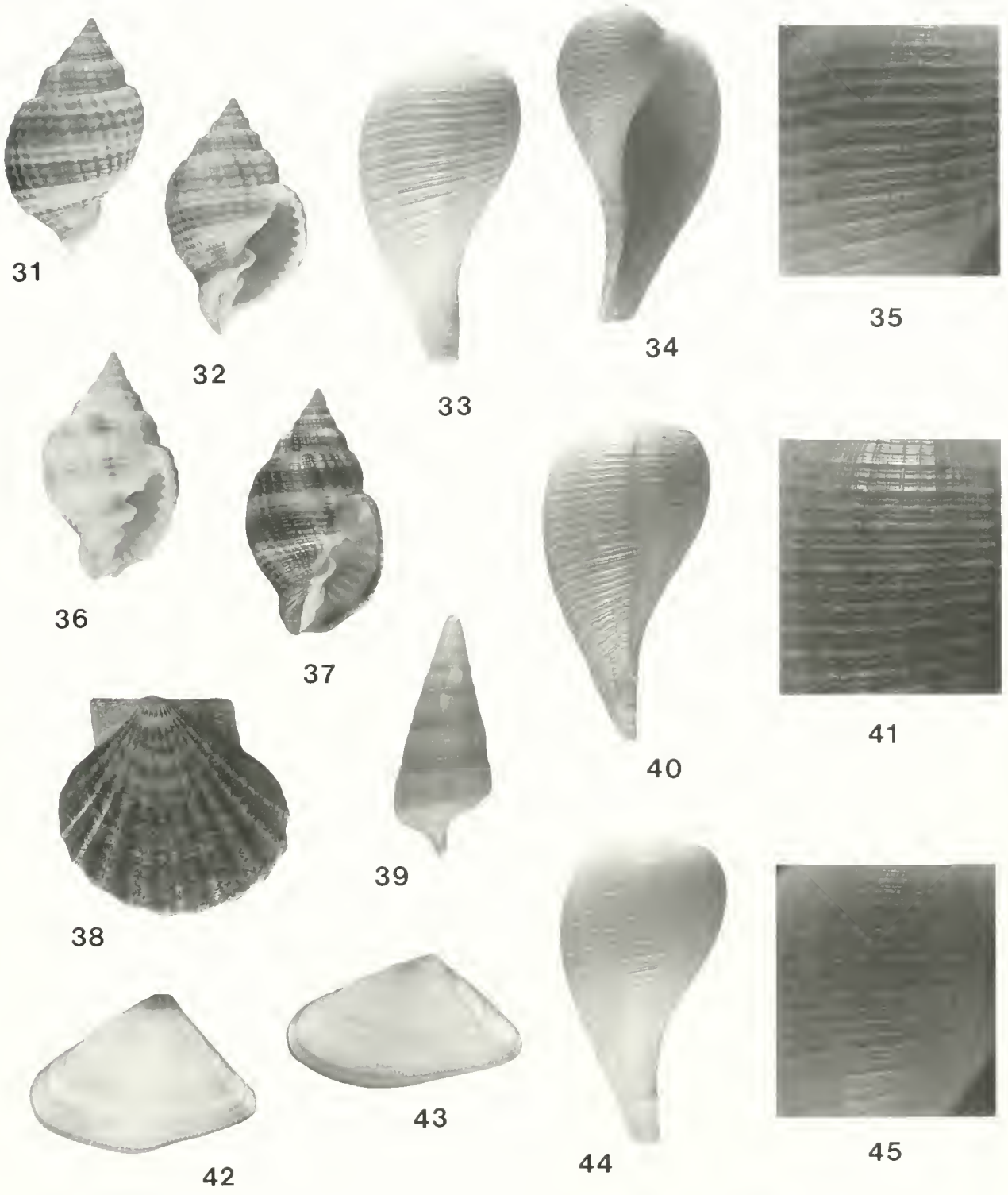
Figures 31–45. Mollusks characteristic of the *Ficus—Pacipecten* and *Hastula—Donax* Assemblages. **31, 32.** *Cancellaria mediamericana* new species, holotype, length 34 mm, **33, 34.** *Ficus villai* new species, holotype, length 67 mm, **35.** Detail of shell sculpture of holotype of *Ficus villai*; **36.** *Cancellaria reticulata* (Linnaeus, 1767), length 27 mm. From beach at Sanibel Is., Florida,



for comparison with *Cancellaria mediamericana;* **37.** *Cancellaria petuchi* Harasewych, Petit & Verhecken, 1992, length 35 mm. Trawled from 25 m depth off Victoria, Espirito Santo, Brazil. for comparison with *Cancellaria mediamericana;* **38.** *Pacipecten leucophaeus* (Reeve, 1852), length 38.5 mm; **39.** *Cerithioclava garciai* Houbrick, 1985, juvenile specimen, length 34 mm; **40.** *Ficus lindae* Petuch, 1988, length 99 mm.Trawled from 20 m depth off the Monges Islands, Gulf of Venezuela, for comparison with *Ficus villai;* **41.** Detail of shell sculpture of *Ficus lindae;* **42.** *Donax striatus* Linnaeus, 1767, length 34 mm; **43.** *Donax mediamericanus* Pilsbry, 1919, length 30 mm; **44.** *Ficus communis* Röding, 1798, length 67 mm. From beach at Sanibel Is., Florida, for comparison with *Ficus villai;* **45.** Detail of shell sculpture of *Ficus communis.*

systems usually contain one or two *Donax* species and only two or three *Strigilla* species.

The other molluscan assemblage found along the Wawa beaches, the *Ficus-Pacipecten* Assemblage, is probably only partially represented, with its community structure data being biased toward those species whose shells most readily accumulate along the shore after storms. Nevertheless, sufficient information exists about this intriguing and unstudied ecosystem, mostly gleaned from beach deposits, to show that this offshore community is, in many ways, as atypical of the Caribbean region as is the *Agaronia—Micromactra* Assemblage of shallower water areas. Characteristic mollusks of the Miskito Coast offshore, subtidal area include:

Gastropods

Turbo castanea Gmelin, 1791
Vermicularia spirata (Philippi, 1836)
Cerithioclava garciai Houbrick, 1985 (Figure 39)
Crepidula convexa Say, 1822
Xenophora conchyliophora (Born, 1780)
Cypraea (Macrocypraea) zebra Linnaeus, 1758
Pseudocyphoma intermedia (Sowerby, 1828)
Naticarius canrena (Linnaeus, 1758)
Polinices hepaticus (Röding, 1798)
Phalium granulatum (Born, 1778)
Distorsio robinsoni Petuch, 1987
Tonna galea (Linnaeus, 1758)
Ficus villai n.sp. (Figures 33, 34, 35)
Chicoreus brevifrons (Lamarck, 1822)
Chicoreus mergus (E.Vokes, 1974)
Vokesimurex cabrittii (Bernardi, 1859)
Vokesimurex garciai (Petuch, 1987)
Talityphis expansus (Sowerby, 1874)
Costanachis veleda (Duclos, 1846)
Nassarius vibex (Say, 1822)
Fasciolaria tulipa (Linnaeus, 1758)
Fusinus dowianus (Olsson, 1954)
Vasum muricatum (Born, 1778)
Voluta lacertina Petuch, 1990
Cancellaria mediamericana n.sp. (Figures 31, 32)
Prunum guttatum (Dillwyn, 1817)
Prunum pruinosum (Hinds, 1844)
Conus aureopunctatus Petuch, 1987
Conus daucus Hwass, 1792
Conus garciai daMotta, 1982
Conus rosemaryae Petuch, 1990
Conus spurius Gmelin, 1791
Terebra taurina Lightfoot, 1786

Bivalves

Arca imbricata Bruguière, 1789
Arca zebra (Swainson, 1833)
Anadara brasiliana (Lamarck, 1819)
Anadara ovalis (Bruguière, 1789)
Barbatia domingensis Lamarck, 1819
Caloosarca notabilis (Röding, 1798)
Atrina seminuda (Lamarck, 1819)
Argopecten gibbus (Linnaeus, 1758)
Pacipecten leucophaeus (Reeve, 1852) (Figure 38)
Lopha equestris Say, 1834
Diplodonta semiaspera (Philippi, 1836)
Chama congregata Conrad, 1833
Laevicardium laevigatum (Linnaeus, 1758)
Mactrellona alata (Spengler, 1802)
Tellina angulosa Gmelin, 1791
Tellina similis Sowerby, 1806
Sanguinolaria cruenta (Lightfoot, 1786)
Chione cancellata (Linnaeus, 1767)
Chione (Lirophora) latilirata (Conrad, 1841)
Chione (Lirophora) paphia (Linnaeus, 1767)
Pitar circinatus (Born, 1778)
Corbula contracta Say, 1822

Because of their thin and lightweight but yet structurally-strong shells, *Ficus villai* n.sp. and *Pacipecten leucophaeus* (Reeve, 1852) (single valves) are collected abundantly along the beach, most often in perfect condition. Judging from its abundance as beach shells, the western Caribbean endemic *Pacipecten leucophaeus* must form dense beds just offshore, much as the closely-related analogue species *Pacipecten tumbezensis* (d'Orbigny, 1846) does along the subtidal areas off western Central America. The Panamic appearance of the Miskito Coast subtidal assemblage is further enhanced by the presence of *Ficus villai* n.sp. (possibly a close relative of the Panamic *Ficus ventricosa* (Sowerby, 1825)) and by *Cancellaria mediamericana* n.sp. (resembling members of the Panamic *Cancellaria obesa* Sowerby, 1832 species complex). The subtidal assemblage also shows a close relationship to the faunas of Caribbean Honduras to the north (Petuch, 1987; Petuch, 1988:155–156) and to Caribbean Panama in the south (Petuch, 1990), especially in containing such distinctive western Caribbean endemics as *Cerithioclava garciai* Houbrick, 1985, *Vokesimurex garciai* (Petuch, 1987), *Fusinus dowianus* Olsson, 1954, *Voluta lacertina* Petuch, 1990, *Conus garciai* da Motta, 1982, *Conus rosemaryae* Petuch, 1990, and *Conus aureopunctatus* Petuch, 1987.

Stations 5 and 6. (*Neritina—Polymesoda* Assemblage)

The Wawa River and its numerous small tributaries expand into three large lagoons before coalescing and narrowing into a single large final channel. These lagoons, the Laguna Yulu-Laguna Karatá complex (to the west of the main Wawa channel) and the smaller Laguna Kauropura (to the east of the main channel) come together near the Salonque de Kauropura, producing a rechannelized Wawa River mouth that empties into the Caribbean Sea approximately 11 km south of Puerto Cabezas. The headwaters of these lagoons are essentially freshwater, becoming brackish in the southern part of Laguna Karatá and gradually becoming more saline at the Salonque de Kauropura. Open oceanic salinity does not appear until well past the Barra de Wawa at the river mouth.

Since these brackish coastal lagoons are virtually unexplored biologically, two different localities were selected within the lagoonal system; one along the slightly brackish southern Laguna Karatá near Karatá Village, and one along the more saline Salonque de Kauropura. The shorelines of the lagoons and final river channel are lined with dense thickets of the red mangrove (*Rhizophora mangle*) (Figure 30) and most of the molluscan fauna is mangrove-associated. Open channel and lagoon bottoms are covered with muddy-sand, and oyster bars occur in deeper areas. Characteristic mollusks from the Karatá and Kauropura estuarine localities include:

Gastropods

Neritina piratica Russell, 1940 (Figure 28)
Neritina reclivata (Say, 1822)
Littorina angulifera (Lamarck, 1822)
Littorina nebulosa (Lamarck, 1822)
Cerithidea pliculosa veracruzensis Bequaert, 1942
Melongena melongena (Linnaeus, 1758)
Melampus coffeus (Linnaeus, 1758)

Bivalves

Crassostrea rhizophorae (Guilding, 1828) (Figure 22)
Crassostrea virginica (Gmelin, 1791) (Figures 26, 27)
Polymesoda placans (Hanley, 1845) (Figure 29)

Although faunistically impoverished, the Wawa estuary is probably typical of the Miskito coastal lagoonal system, and shows a degree of endemism. The presence of *Neritina piratica* Russell, 1940, *Cerithidea pliculosa veracruzensis* Bequaert, 1942, and *Polymesoda placans* (Hanley, 1845), all of which are restricted to the western Caribbean, demonstrates the close relationship of the Wawa assemblage with those to the north (Honduras) and to the south (Costa Rica).

Within the final channel of Barra de Wawa, a large, slender variant of *Crassostrea virginica* (Gmelin, 1791) (resembling the Floridian Pleistocene *C.labelleensis* Olsson & Harbison, 1953) forms massive reeflike bars in deeper, more saline water. The large carnivorous gastropods *Thais floridana* (Conrad, 1837) and *Melongena melongena* (Linnaeus, 1758) are common on these bars and are the primary predators of the oysters.

SYSTEMATIC SECTION

The holotypes and paratypes of the following new species are deposited in the type collection of the Division of Mollusks, Section of Invertebrate Zoology, the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania. A voucher collection of at least one specimen of each species listed has also been deposited in the main collection of the Carnegie Division of Mollusks.

SYSTEMATICS

Gastropoda
Caenogastropoda
Tonnoidea
Ficidae
Ficus Röding, 1798
Ficus villai new species
(Figures 33, 34, 35)

Description: *Ficus* of average length for genus (adults av. 62 mm), elongated, pyriform, belonging to *Ficus communis* Röding, 1798 species complex. Shell ornamented with thick spiral cords that are better developed than longitudinal cords. Spiral cords colored with irregular, small, pale brown and white dots. Some specimens with broad, dark brown longitudinal flammules, producing "zebra" pattern. Shell thin, lightweight, but structurally strong. Shoulder rounded, gently sloping. Suture depressed, subcanaliculate. Spire elevated above shoulder line, slightly scalariform. Shell surface covered with evenly-spaced, intersecting longitudinal and spiral cords, producing fenestrate patterns. Spiral cords much stronger and better-developed than longitudinal cords, approximately four times as thick (Figure 35). Thinner, fine secondary cord present between each pair of thick primary cords, with secondary cord being approximately as thick as thin longitudinal cords. One or two extremely fine, hairlike, tertiary spiral cords present on either side of secondary spiral cord, giving areas between thick primary cords a silky appearance. Average specimen (based on type lot) with 26 large primary cords on combined body whorl and siphonal canal. General apertural shape elongately ovate, tapering gradually into open siphonal canal. Aperture proportionally wide, approximately equal in size to ventral half of body whorl. Edge of labrum in adult specimens (such as holotype) thickened, reinforced with thin, white, callus-like deposit. Well-preserved specimens show slight undulation along labral edge, with raised areas corresponding to edges of large, primary spiral cords. As typical of all known members of *Ficus communis* species complex, protoconch bulbous, mammillate in appearance, smooth, consisting of 1½ whorls. In fresh specimens, color somewhat variable, generally tan or pale brown with large, wide brown, longitudinal flammules of varying intensities (such as on holotype, Figures 33, 34). On many specimens (such as holotype), primary cords exhibit faint pattern of alternating pale whitish-tan and light brown elongated spots. Depressed subsutural area whitish-tan, paler than rest of body whorl. Anterior half of siphonal canal light brown, darker than body whorl. Protoconch pale whitish-tan. Interior of aperture brown, becoming lighter in color toward labral edge, and with prominent, widely-spaced dark brown stripes that correspond to external primary spiral cords. Columellar side of siphonal canal white. Interior of siphonal canal characteristically dark brown, several shades of intensity darker than aperture interior or body whorl exterior.

Type material: Holotype (CMNH 17339) length 67 mm, width 36 mm; Paratype lot (7 specimens) (CMNH 37340) ranging from length 44 mm, width 27 mm, to length 77 mm, width 44 mm. All type material from the type locality.

Type locality: On beach, high tide line, Barra de Wawa, northern side of Wawa River mouth (Station 3), Miskito Coast, Nicaragua.

Additional localities: Fragmentary specimens were also seen on beach, high tide line, southern side of Wawa River mouth (Station 4), near Wawa Village, Miskito Coast, Nicaragua.

Distribution: At present, collected only from the area of the Wawa River mouth, Miskito Coast, Nicaragna, but may extend from the Honduran Miskito Coast, near Cabo Gracias a Dios, southward to Bluefields, Nicaragua. Discussions with local shrimpers have indicated that *Ficus villai* n.sp. is frequently taken in shrimp nets during shallow (app. 15–20 m depth) trawls off the Cabo Gracias a Dios coast, and that the local fishermen are familiar with this locally-common species. Broken, fragmentary specimens of *Ficus villai* were also collected at Puerto Cabezas (Station 2), but the condition of these was too poor to be part of the type lot.

Etymology: Named for Dr. Jaime Villa, Professor of Biological Sciences, Florida Atlantic University, who assisted me in collecting along the Wawa River area and who was instrumental in securing my involvement in the C.C.C. Miskito Coast research project.

Remarks: As presently understood, the *Ficus communis* complex consists of three shallow water species with disjunct distributions within the tropical and warm-temperate western Atlantic; *Ficus communis* Röding, 1798, (Figures 44, 45) a Carolinian Province, warm-temperate species that ranges from Cape Hatteras, North Carolina to Miami, Florida, and from Naples, Florida around the Gulf of Mexico to Isla Contoy, Yucatán, Mexico, and two tropical, Caribbean Province species, *Ficus villai* n.sp., restricted to Miskitia, and *Ficus lindae* Petuch, 1988 (Figures 40, 41), restricted to northern Colombia and the Gulf of Venezuela area. These distributions are shown in Figure 46.

Of the two previously-described species, *Ficus villai* is most similar, in both shell size and thickness, to the Carolinian *F.communis*. The new species differs from its common and well-known congener in the following ways; *1. shell shape—F. villai* is a more slender shell with a higher, stepped spire; *2. shell sculpture*—the new species has a very distinct sculpture pattern composed of thick, prominent, high-relief, primary spiral cords that dominate the sculpture (Figure 35), while *F. communis* has a much lower-relief pattern composed of weaker primary cords that are nearly equal in size to the secondary cords (Figure 45); *3. shell color—F. villai* is a much darker-colored shell, generally with dark longitudinal flammules (Figure 33) and always with a prominent, dark brown end to the siphonal canal, while *F. communis* is a lighter-colored shell, lacking both the longitudinal, "zebra"-type flammules and the darkly-colored anterior end.

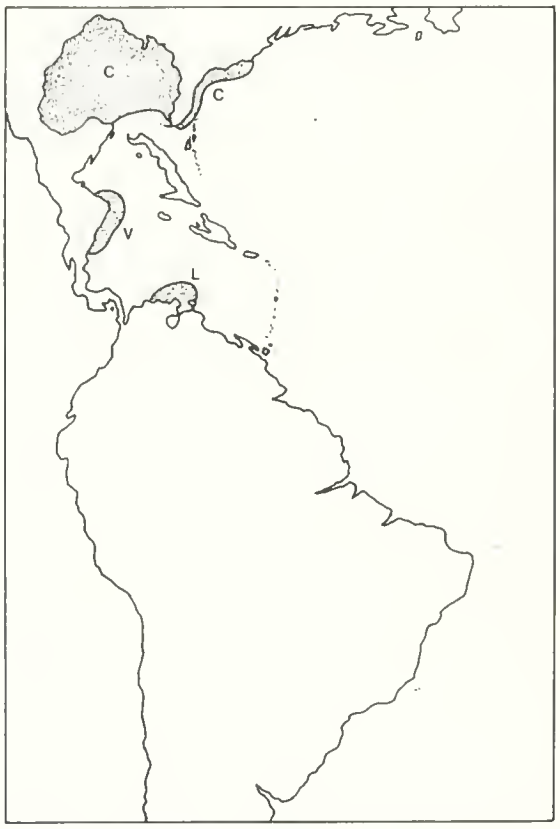


Figure 46. Distributions of the shallow water *Ficus* Röding, 1798 species of the western Atlantic. C = *Ficus communis* Röding, 1798; V = *Ficus villai* new species; L = *Ficus lindae* Petuch, 1988.

The remaining member of the complex, *Ficus lindae* is the least similar to the new species, differing in having a larger and much thinner, almost paperlike, shell. As in the comparison with *F. communis*, *F. villai* also differs from *F. lindae in* three distinct ways; *1. shell shape*—the new species has a proportionally more slender, less inflated shell with a higher, more elevated spire; *2. shell sculpture—F. villai* exhibits a sculpture pattern of dominant, high-relief primary spiral cords with interstitial smaller secondary and tertiary spiral cords, while *F. lindae* (Figure 40) has much reduced, much lower-relief primary spiral cords, a single reduced, secondary spiral cord, and no tertiary cords; *3. shell color*—although both species have similar brown shells with longitudinal darker brown flammules, *F. villai* has a pale, whitish-tan subsutural area and a dark brown siphonal end, both of which are lacking in *F. lindae*.

The new species also shows some morphological similarity to *Ficus carolae* Clench, 1945, a deep water (200 m depth) species from off the Florida Keys and Campeche Banks of Yucatan, Mexico. This bathyal ficid

somewhat resembles *F. villai*, particularly in shell size, shape, and proportions, but differs in having less-developed primary spiral cords and in having a paler-colored shell that is conspicuously and characteristically marked with scattered large, elongated, dark brown spots. *Ficus carolae* may represent a deep water, continental slope-dwelling offshoot of the shallow water *Ficus communis* complex. The two other known deep water western Atlantic ficids, *F. atlantica* Clench & Aguayo, 1940 (900 m depth off central Brazil) and *F. howelli* Clench & Aguayo, 1940 (200–400m depth from Cuba to Trinidad), both have extremely inflated, paper-thin shells, short, stubby siphonal canals, and regularly-arranged, darkly-spotted color patterns. These two species, together, differ greatly from the *F. communis* complex, and appear to represent a separate, distinct, unrelated group.

With the discovery of the Miskitian *Ficus villai*, it is now known that the western Atlantic houses six species of Ficidae. Of these, three live in deep water (200–400 m), continental slope areas and three prefer shallow water, neritic environments. The three shallow water species can be separated as follows (+ = present, − = absent):

	F. villai	*F. communis*	*F. lindae*
1. prominent 1° spiral cord	+	−	−
2. 2° and 3° spiral cords	+	+	−
3. dark longitudinal flammules	+	−	+
4. white spots on spiral cords	+	+	+
5. pale subsutural area	+	−	−
6. dark siphonal end	+	−	−

Cancellarioidea
Cancellariidae
Cancellaria Lamarck, 1799
Cancellaria mediamericana new species
(Figures 31, 32)

Description: Typical western Atlantic *Cancellaria* s.s., of average length for genus (adults av. 35 mm), crudely biconic, with inflated body whorl. Shoulder angled, with flattened subsutural area. Anterior canal short, open. Inner lip along columella with 2 columellar and 1 siphonal folds. Posteriormost columellar fold largest, overlying siphonal fasciole. Body whorl and spire whorls with heavy, coarse cancellate sculpture. Shell thick, structurally strong, reinforced by heavy cancellate sculpture. Outline of body whorl and spire whorls rounded. Edge of shoulder acute, marked with carina-like spiral cord. Flattened subsutural areas give scalariform appearance to spire. Shell surface covered with evenly-spaced, intersecting longitudinal and spiral cords, producing even cancellate sculpture. Cords of equal size and shape. Intersection of cords producing low, rounded bead, giving shell surface pebbly appearance. Holotype with 33 longitudinal cords and 14 spiral cords on body whorl. Aperture proportionally large, broad, semielliptical in shape. Inner edge of labrum with 13 large, thin cords that extend into aperture.

Figure 47. Distributions of the geographically-restricted species of *Cancellaria* Lamarck, 1799 (*sensu stricto*) in the western Atlantic. R= *Cancellaria richardpetiti* Petuch, 1987; A = *Cancellaria adelae* Pilsbry, 1940; M = *Cancellaria mediamericana* n.sp.; P = *Cancellaria petuchi* Harasewych, Petit & Verhecken, 1992. The distribution of the widespread *Cancellaria reticulata* (Linnaeus, 1767) is not shown.

Labral cords disappear in interior of aperture. Entire columellar region overglazed with thin callus. Callus thicker along anterior end, thinning toward posterior end. Both columellar folds and single siphonal fold with single large, flattened keel. Posteriormost and largest fold with very faint, poorly-developed secondary ridge along anterior side. Protoconch paucispiral in form, composed of 2½ low, inflated, glassy whorls. Protoconch of holotype deviated from main shell axis by approximately 15° (Figure 48). Base shell color pale cream-white. Body whorl with 3 wide, evenly-spaced, continuous dark reddish-brown bands, one around anterior end, one just anterior to mid-body, and one around shoulder. Spire whorls with single wide, reddish-brown band. Anterior tip of shell, anterior canal, and siphonal fasciole pale yellow-tan. Protoconch pale cream-white. Columellar and siphonal folds white.

Type material: Holotype, (CMNH 47341) length 34 mm, width 20.5 mm; Paratypes, (CMNH 47342) (2 specimens), length 34 mm, width 20 mm and length 36 mm, width 22 mm. All type material from the type locality.

Type locality: On beach, high tide line, Barra de

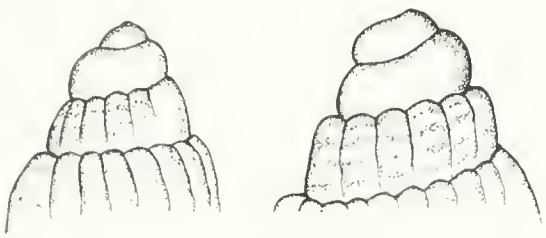


Figure 48. Detail of protoconchs of *Cancellaria* species. (Left) *Cancellaria reticulata* (Linnaeus, 1767), drawn from specimen from Sanibel Is., Florida (Figure 44). (Right) *Cancellaria mediamericana* n.sp., drawn from holotype (Figures 31, 32). Note proportionally larger size and flexure away from shell axis of *C. mediamericana*.

Wawa, northern side of Wawa River mouth (Station 3), Miskito Coast, Nicaragua.

Distribution: At present, known only from the area of the Wawa River mouth, Miskito Coast, Nicaragua, but may extend from the Honduran Miskito Coast, near Cabo Gracias a Dios, southward to Bluefields, Nicaragua. A specimen in the private collection of Mr. Leonard Hill, Miami, Florida, reportedly taken by commercial shrimpers from off Cabo Gracias a Dios, supports a wider range for the new species.

Etymology: "*mediamericana*", "Central American," in reference to the confined range of the new species along the eastern coast of Central America.

Remarks: *Cancellaria mediamericana* n.sp. is the newest member of a characteristic western Atlantic species complex centered around the widespread *Cancellaria (s.s.) reticulata* (Linnaeus, 1767) (Figures 36). That well-known and common species ranges from North Carolina, throughout the Gulf of Mexico, along the Antilles Arc, and southward to northern Brazil. Besides *C. reticulata* and *C. mediamericana*, the complex also includes three other species with restricted geographical ranges (Figure 47). These are: *Cancellaria richardpetiti* Petuch, 1987 (100–200m depth off western Florida), *Cancellaria adelae* Pilsbry, 1940 (carbonate sand areas, 1–10 m depth, Florida Keys), and *Cancellaria petuchi* Harasewych, Petit & Verhecken, 1992 (central and southern Brazil) (Figure 37). Of the members of the complex, *C. mediamericana* is most similar to the widespread *C. reticulata*, but differs in the following ways; *1. shell shape*—the new species has a more inflated shell with a wider aperture; 2. *columella*—*C. mediamericana* has only two columellar folds, with the large posteriormost fold being flattened and keel-like, while *C. reticulata* has three folds with the large central fold being characteristically bifid in form; 3. *protoconch*—the protoconch of the new species is proportionally large, inflated, and bulbous with a slight flexure away from the main shell axis, while that of *C. reticulata* is proportionally much smaller (Figure 48), tightly cylindrical in form, composed of three whorls, and is aligned with the main shell axis; *4. color*—in the new species, the shell is marked with three solid color bands, while in *C. reticulata*, the color bands are discontinuous, broken into a series of separate, large, rectangular maculations.

Cancellaria mediamericana is also similar to the Brazilian *C. petuchi* Harasewych, Petit & Verhecken, 1992 (Figure 37) but differs in the following ways; *1. shell shape*—although both species have widely inflated body whorls, *C. mediamericana* has a sharply-angled shoulder and a flattened, planar subsutural area, while *C.petuchi* has a distinctly rounded shoulder; 2. *shell sculpture*—while *C. mediamericana* has a sharp, strong reticulate sculpture pattern that persists onto the body whorl, *C. petuchi* has a reduced sculpture pattern of low, rounded ribs that become obsolete on the body whorl. Both species, although widely separated geographically, have similar inflated, bulbous protoconchs, triple-banded continuous color pattern, and have only two, flattened, keel-like columellar folds.

The other two species of the complex, *C.adelae* Pilsbry, 1940 and *C. richardpetiti* Petuch, 1987, are both more similar to *C.reticulata* than to *C. mediamericana*. The deep water, bathyal *C.richardpetiti* is a distinctly elongated shell with a high, protracted spire. The Florida Keys endemic *C. adelae*, although generally similar to *C. reticulata*, has reduced shell sculpture, producing a smooth body whorl like that of *C. petuchi*. Both species, *C.richardpetiti* and *C. adelae*, however, have three columellar folds and have bifid, large central folds. In the last character, particularly, these two species much more closely resemble *reticulata* than *C. mediamericana*. For a comparison of the shell morphologies of *C. reticulata*, *C. adelae*, and *C. petuchi*, see Harasewych, Petit & Verhecken (1992). The widespread Caribbean, Miskitian, and Brazilian *Cancellaria* species can be separated as follows (+ = present, − = absent):

	C. mediamericana	*C. reticulata*	*C. petuchi*
1. inflated protoconch	+	−	+
2. solid color bands	+	−	+
3. columellar callus	+	−	+
4. 3 columellar folds	−	+	−
5. 2 columellar folds	−	+	+
6. bifid central fold	−	+	−
7. angled shoulder	+	+	−

Conoidea
Conidae
Conus Linnaeus, 1758
Leptoconus Swainson, 1840
Conus (Leptoconus) paschalli new species
(Figures 2, 3)

Description: *Conus* of smaller-than-average length for subgenus *Leptoconus* (adults av. 24 mm), with stocky body whorl, wide shoulder, and proportionally low spire. Shoulder sharply-angled, subcarinated. Spire whorls flattened, noncanaliculate. Operculum unknown. General shell form subpyriform, with convex sides on body

whorl. Body whorl tapers abruptly anteriorly, pinching-off noticeably to produce narrow siphonal area. Spire whorls slightly raised above suture line, giving stepped appearance to overall spire. Body whorl smooth and polished, marked with numerous very faint longitudinal growth lines. Spire whorls marked with very numerous, closely-spaced crescent-shaped threads. Anterior one-third of body whorl encircled with 9–11 evenly-spaced, deeply-impressed spiral sulci. Aperture proportionally narrow, widening slightly on anterior one-half of shell. Protoconch unknown, missing on holotype and type lot. Based upon proportions of broken early whorls, protoconch probably large and bulbous. Base color white or pale yellowish-white, overlaid with 8–10 evenly-spaced spiral bands of large orange dots and blotches. In some cases, such as in holotype (Figures 2, 3), dots and rectangular blotches coalesce to produce large, widely-spaced orange longitudinal flammules arranged in "zebra" pattern. Clear white band, devoid of markings, except for few small spots, present just anteriorward of midbody line. Clear band separates dots and longitudinal flammules into two wide sections, one extending from shoulder to below midbody line, and a narrower one extending around anterior end of shell. Anterior tip of shell very pale pinkish-lavender. Spire whorls white, marked with widely spaced, orange, crescent-shaped flammules. Early whorls (and presumed protoconch) pale orange. Interior of aperture white. Based on small patch still adhering to outer lip of holotype (later removed by cleaning in sodium hypochlorite), periostracum is thick, heavy, brown in color, marked with very fine, longitudinal striae.

Type material: Holotype, (CMNH 47344) length 26 mm, width 14 mm; Paratypes (7 specimens), (CMNH 47345) ranging from length 20 mm, width 11 mm, to length 27 mm, width 14.5 mm. All type material from the type locality.

Type locality: On beach flat, low tide, southern side of Bragman's Bluff (Station 1), approximately 2.5 km north of Puerto Cabezas, Miskito Coast, Nicaragua.

Distribution: At present, known only from the beach areas near Bragman's Bluff and Puerto Cabezas, Nicaragua, but may extend southward to Bluefields, Nicaragua.

Etymology: Named for Dr. Norman Paschall of Largo, Florida, who assisted me in collecting in the Bragman's Bluff area.

Remarks: Of the known Caribbean small *Leptoconus* species, *Conus paschalli* is most similar to *Conus portobeloensis* Petuch, 1990 from the San Blas Islands region of Panama. The new species differs from its southern congener in the following ways; *1. shell shape*—*C. paschalli* is a smaller (av. 24 mm) species than *C. portobeloensis*, with a stockier, proportionally shorter, and more pyriform body whorl; the shoulder of *C. paschalli* is sharply-angled, almost carinated, while *C. portobeloensis* has a more rounded shoulder edge with only the faintest hint of a carina; *2. spire*—the spire of of *C. paschalli*, although low like that of *C. portobeloensis*, is distinctly stepped, with the spire whorls being slightly raised above each subsequent suture line; the spire of the Panamanian species has depressed sutures, producing a gradually-sloping spire outline instead of a scalariform one; the spire whorls are planar on the new species, while those of *C. portobeloensis* are sloping and faintly canaliculate; *3. shell sculpture*—*C. paschalli* has a smooth shell with faint longitudinal striae, while the shell of *C. portobeloensis* is distinctly sculptured with fine spiral threads and striae; the anterior third to the body whorl of *C.paschalli* is encircled with 9–11 large, deeply-incised sulci, while the anterior third of *C. portobeloensis* is encircled by at least 20 thin, faint raised cords and an equal number of shallow, thin sulci; *4. color*—while both species have a color pattern composed of spiral lines of dots and large coalescing longitudinal flammules, *C. paschalli* has fewer rows of dots and the individual dots are proportionally larger; the anterior tip of *C. portobeloensis* is pale yellow-orange while that of *C. paschalli* is pale pinkish-lavender. *5. habitat*—judging from the type locality, the new species prefers muddy sand localities in shallow muddy water areas along the river effluent zone of the Miskito Coast of Nicaragua; *Conus portobeloensis*, on the other hand, lives in an offshore (30 m depth) carbonate substrate—clean water environment (see Petuch, 1990:68) off the Colón and San Blas coasts of Panamá. Neither species, nor anything resembling them, has been collected along the intervening clean sandy coast of Costa Rica (Houbrick, 1968), demonstrating geographical and ecological separation.

Bivalvia
Pteriomorpha
Arcoida
Arcidae
Noctia Gray, 1857
Noctia (s.s.) lindae new species
(Figures 9, 10)

Description: Shell small for genus (adults av. 25 mm), equivalve elongated, subtrigonal in shape. Posterior end only slightly expanded, truncated, sharply angled, tapering to sharp point. Angled posterior truncation bordered by large, prominent posterior ridge that runs from umbones to posterior tip. Shallow medial depression present on posterior end above posterior ridge. Umbones placed extremely forward, in anterior one-third of shell. Anterior end not expanded, rounded, without angled ridge. Shell surface with 30–32 evenly-spaced, low, wide, rounded primary radial ribs. Thin, rounded secondary radial rib present between each pair of wide primary ribs. Secondary rib bisected by fine incised line. Primary and secondary radial ribs covered by and intersecting with very fine, closely-packed concentric growth lines, giving ribs slightly roughened appearance. Intermittent

large concentric growth lines present, corresponding to periodic cessations in shell growth. Shell margin and inner margin marked with 30–32 sharp, well-developed crenulations that correspond to thin secondary ribs. Beaks large, prominent, angular, projecting above hinge line. Umbones well-developed, recurved. Beaks and umbones strongly opisthogyrate. Hinge line straight, with coarse taxodont dentition. Posterior teeth larger than anterior teeth. Hinge ligament elongated, broad, with transverse ligamentary grooves at right angles to hinge line. Ligamentary grooves 7–8 in number, placed anteriorly to umbones. Anterior muscle scar proportionally small, oval, at extreme anterior end. Posterior muscle scar proportionally large, oval, formed at base of long, narrow, low flange. Posterior flange extends upward into umbonal interior. Pallial line weakly developed, straight, following edge of shell margin just above marginal crenulations. Shell pale-to-bright lemon-yellow or cream-orange, with posterior end and area above posteroventral angle being darker yellow-orange. Umbones and beaks brightly colored, generally dark reddish-orange or bright cherry red. Shell interior pale yellow or yellowish-white, with some specimens (holotype and 6 paratypes) having darker yellow-orange stain deeper within. Occasional specimens (such as one left valve paratype) with dark red-orange stain that extends from umbonal interior to posterior margin. Periostracum (Partially preserved on two left valve paratypes; removed from holotype pair by soaking in sodium hypochlorite solution) thick, black, coarsely lamellose, marked with thin concentric striae. Periostracum eroded off of beaks of all specimens examined.

Type material: Holotype, (CMNH 47367) length 25.5 mm, width 15 mm; Paratypes, (12 single valves, CMNH 47343), ranging from length 20 mm, width 13 mm to length 29 mm, width 18 mm. All type material from the type locality.

Type locality: On lower beach flat at low tide, southern side of Bragman's Bluff (Station 1), approximately 2.5 km north of Puerto Cabezas, Miskito Coast, Nicaragua.

Distribution: At present, known only from the beach area near Bragman's Bluff, Puerto Cabezas, Nicaragua, but may possibly be found southward along the Miskito Coast.

Etymology: Named for my wife, Linda Joyce Petuch.

Remarks: *Noetia lindae* is the first member of its genus (s.s.) to be recorded from the Caribbean region, and only the second species of *Noetia* s.s. to be found in the western Atlantic. The other species, *Noetia bisulcata* (Lamarck, 1819) occurs along eastern South America, from Surinam to Uruguay (range and illustration in Rios, 1975: fig. 949). No other *Noetia* s.s. is known to occur in the area between *N. lindae* and *N. bisulcata*. The larger *Noetia ponderosa* (Say, 1822) from the Carolinian Province belongs to (and is the type of) the subgenus *Eontia* MacNeil, 1938, and represents a different and separate *Noctia* lineage. The Panamic *Noctia reversa* (Sowerby, 1833) and *Noctia olssoni* Sheldon and Maury, 1922 are very similar to *N. lindae*, and the new Caribbean species appears to be intermediate in shell form between its two Pacific relatives; having the more elongated shape of *N. olssoni* and the strong, prominent posterior ridge and high beaks of *N. reversa*.

In general shell shape and size, *Noctia lindae* is most similar to the South American *N. bisulcata*, but differs in the following ways; *1. shell shape—N. lindae* is a much more elongated species with a projecting, distinctly pointed posterior end, while *N. bisulcata* has a more ovate shell shape with a wide, blunt posterior end; the beaks of the new species are located much more anteriorly, within the anterior one-third of the shell, whereas the beaks of *N. bisulcata* are more medially located, almost at the midbody line; the dorsal posterior area immediately above the posterior ridge is flattened in *N. lindae*, while in *N. bisulcata* the posterior dorsal area is raised and laterally flattened; *2. color—N. lindae* is a much more colorful shell than its southern relative, often exhibiting a bright yellow or yellow-orange shell with red umbones, while *N. bisulcata* has a more subdued shell color, being white or pale yellow-white with light orange umbones.

Pterioida
Pectinoidea
Plicatulidae
Plicatula Lamarck, 1801
Plicatula miskito new species
(Figures 16, 17, 18, 9)

Description: Shell small for genus (holotype 13 mm), ovately subtrigonal in shape, flattened, with right valve attached to substrate. Auricles present but poorly-developed, with posterior auricle larger and wider than anterior auricle. Interior porcellaneous. Hinge line straight. Exterior of free (left) valve with very fine, raised concentric lines that become stronger and more lamellose toward shell margin. Area near beaks decorated with 18 very fine beaded radial ribs. Radial ribs flatten and disappear halfway between beak and shell margin. Shell margin faintly crenulate. Beak poorly-developed, almost planar, with small, faint sharply-pointed umbo projecting only slightly above hinge line. Entire hinge structure proportionally large, typically spondyloid, with narrow, small, elongated chrondrophore. Chondrophore pit of upper (left) valve flanked by two crural ridges, each with single, smooth ball-type teeth. Chondrophore pit of bottom (right) valve flanked by two elongated sockets and two small elongated teeth. Single adductor scar posterior to center of shell, almost circular in shape. Pallial line deeply incised, located subcentrally, following shell margin. Exterior of free (left) valve white with numerous fine, radiating, pale reddish-brown lines and large, scattered, dark reddish-brown spots. Shell margin marked with large, prominent, equally-spaced, dark reddish-

brown streaks. Subumbonal area stained pale tan. Umbo reddish-tan. Attached (right) valve pure white. Interior of left valve white with large pale tan stain, extending from adductor scar to umbonal area. Margin of shell interior of left valve marked with prominent, equally-spaced dark reddish-brown streaks, corresponding to those seen on shell exterior. Ball-and-socket teeth of both valves pale tan.

Type material: Holotype (pair) (CMNH 47366) length 13 mm, width 5 mm.

Type locality: On lower beach flat at low tide, in shell rubble bed, southern side of Bragman's Bluff (Station 1), approximately 2.5 km north of Puerto Cabezas, Miskito Coast, Nicaragua. Holotype found attached to interior of *Noctia lindae* n.sp. valve (Figures 18, 19).

Distribution: At present known only from shell rubble beds at Bragman's Bluff, Puerto Cabezas, Nicaragua.

Etymology: Named for the Miskito Indians, as a noun in apposition.

Remarks: *Plicatula miskito* n.sp. is only the second-known representative of its genus in the western Atlantic, and is the first *Plicatula* to be collected on the Miskito Coast. The other Atlantic member, *Plicatula gibbosa* Lamarck, 1801, which ranges from North Carolina to Brazil, is an abundant but very different-appearing species and does not seem to be closely related. *Plicatula miskito* differs from its widespread and well-known congener in the following ways; *1. size—P. gibbosa* is a much larger species, averaging 25 mm in length (Abbott, 1974: 450), while *P. miskito* is a much smaller animal, with the holotype being only 13 mm in length; *2. shape and sculpture*—the common *P.gibbosa* is a very rugosely-sculptured species with 5–7 prominent, high, raised plications that give the shell a strongly ribbed appearance (hence the common name, the "kitten's paw"), while the shell of *P. miskito* lacks the raised plicae having, instead, fine beaded radial riblets near the umbo; the shell margin and commissure of *P. miskito* are relatively straight and flattened while those of *P. gibbosa* are strongly undulate.

Morphologically, the new species is most similar to *Plicatula penicillata* Carpenter, 1857 from the Panamic Province, and its presence in the Miskitian malacofauna further underscores the Pacific faunal affinities of the Nicaraguan Caribbean coastal region. The two species are strikingly similar, particularly in size, shape, and color pattern. Both species exhibit the distinctive and characteristic large dark streaks along the shell margin and both have the large tan stain within the shell interior. *Plicatula miskito* differs from *P. penicillata* primarily in the surface sculpture of the free valve; while the new species is relatively smooth, with only faint concentric laminae and radial riblets, its Panamic congener has a more crenulate, rougher, surface, often decorated with small ribs and spines. Otherwise, the two species are extremely close and they form an impressive example of a previously-unknown Panamic-Caribbean sibling species pair.

Heterodonta
Veneroida
Mactroidea
Mactridae
Mactra Linnaeus, 1767
Mactra inceri new species
(Figures 7, 8, 11)

Description: Shell typically mactrid in form, thin, fragile, with convex, inflated valves, of average size for genus. Shell shape generally oval-subtrigonal, with high, pointed umbones and slightly concave posterior-dorsal area. Faint, low, rounded keel borders posterior-dorsal area and posterior margin of umbones. Posterior end slightly pointed, anterior end rounded. Beaks placed slightly anterior to shell midline (based on total shell length). Lunular region wide, deeply impressed. Entire shell exterior covered with very fine, closely-packed concentric growth lines, giving shell silky texture. Growth lines become coarser toward shell margin. Beaks large, prominent, trigonal in shape, projecting above hinge line. Umbones highly recurved, strongly prosogyrate. Resilifer proportionally large, trigonal in shape, with apex of triangle bent anteriorally. Resilifer set in large, cup-shaped chondrophone that overhangs umbonal region, producing deep subumbonal cavity. Edges of resilifer-chondrophore complex bounded by thin, raised, slightly concave shelly lamina. Cardinal teeth prominent, with posterior flange overhanging resilifer. Lateral teeth thin, elongated, bladelike, with anterior lateral tooth having projecting, trigonal flange. Anterior adductor scar near extreme anterior margin of shell, thin, elongated in shape. Posterior scar nearly circular in shape, located near extreme posterior shell margin. Pallial line prominent, sinusoidal in form, with long, deep, sublinguiform pallial sinus. Pallial sinus extends horizontally well past shell midline (see Figs. 8, 11). Shell exterior and interior uniform pale cream-white. Periostracum (Present only as fragmentary remnants along margin of holotype valve) pale yellow-tan, thin, translucent, with silky texture.

Type material: Holotype, (single right valve) (CMNH 47338), length 35.5 m, width 41 mm; Figured paratype, (single right valve, CMNH 47346), length 24 mm, width 27 mm; Paratypes, (3 single valves, CMNH 47350), ranging from length 25 mm, width 28 mm to length 33 mm, width 36 mm. All type material from the type locality.

Type locality: On lower beach flat at low tide, southern side of Bragman's Bluff (Station 1), approximately 2.5 km north of Puerto Cabezas, Miskito Coast, Nicaragua.

Distribution: At present, known only from the beach area near Bragman's Bluff, Puerto Cabezas, Nicaragua, but may possibly be found southward along the entire Miskito Coast.

Etymology: Named for Dr. Jaime Incer, director of IRENA, Managua, Nicaragua, in thanks for his assistance and support of my research while I worked along the Miskito Coast.

Remarks: *Mactra inceri* is the first species of *Mactra* (s.s.) to be reported from the Caribbean Basin. The only other known western Atlantic member of the genus is *Mactra iheringi* (Dall, 1897), which ranges from Venezuela (Weisbord, 1964:381–382) southward to Santa Catarina, Brazil (Rios, 1975:236) and, prior to the discovery of the Miskitian species, the genus *Mactra* (s.s.) was conspicuously absent from northern South America, eastern Central America, and the West Indian Arc. Interestingly enough, the subgenus *Mactrotoma* (typified by *Mactra fragilis* Gmelin, 1791), which is the common Caribbean representative of the Mactridae, was not collected along the Miskito Coast but was replaced by the nominate genus.

Although similar to the South American-Brazilian *Mactra iheringi*, *M. inceri* can be readily distinguished by the following characters; *1. shell shape*—The new species has a less-elongated, more rounded and truncated anterior and; because of this truncated appearance, the umbones of *M. inceri* are located slightly anterior to the midbody line, while those of *M. iheringi* are almost exactly centrally located, directly on the midbody; *2. form of the lunule*—in *M. inceri*, the lunule is distinctly depressed, producing a noticeable concavity along the anterior-dorsal area immediately anterior to the umbones; in *M.iheringi*, the lunular area is simply flattened, producing a straight, sloping surface; *3. pallial sinus*—in *M. iheringi*, the sublinguiform pallial sinus extends horizontally to, or a little beyond, the midbody line (Dall, 1897; Weisbord, 1964:381), while in *M. inceri*, the pallial sinus extends well beyond the midbody line (Figures 8, 11) occupying fully two-thirds of the shell interior; this enlarged pallial sinus demonstrates that *M. inceri* has longer siphons than does its southern congener and lives more deeply buried in the substrate.

Micromactra Dall, 1894
Micromactra miskito new species
(Figures 12, 13)

Description: Shell of average size for genus (av. 27 mm), elongated, thin, fragile, with beaks centrally located. Anterior dorsal margin of shell, immediately anterior to beaks, nearly straight, with only slightest hint of concavity. Anterior end rounded, posterior end pointed but angularly truncated. Low but sharp angular ridge present along entire posterior dorsal edge of both valves. Beaks and umbonal area of shell exterior characteristically sculpted with 6–15 large, prominent, undulating waves. Surface of exterior smooth, shiny, covered with very fine, closely-packed concentric growth lines, giving shell faintly silky appearance. Large umbonal undulations also covered by fine concentric growth lines. Very fine, thin, evenly-spaced radial lines present on anterior one-half of shell. Beaks large, prominent, projecting well above hinge line, roughly trigonal in shape. Umbones highly recurved, strongly prosogyrate. Resilifer trigonal in shape, with apex tipped anteriorly, set in small cup-shaped chondrophone. Cardinal teeth distinctly "V"-shaped. Lateral teeth elongated, bladelike. Anterior adductor scar near extreme anterior margin of shell, oval in shape. Posterior scar of approximately equal size and shape, located near extreme posterior shell margin. Pallial line sinusoidal in form, with short, rounded, wide, pallial sinus. Pallial sinus extends horizontally only about one-third of shell interior. Shell exterior and interior uniform translucent white. Periostracum thin, smooth and silky, adherent, pale straw colored, generally missing on umbones.

Type material: Holotype, (single right valve) (CMNII 47364), length 30 mm, width 19 mm; Paratypes, (5 single valves, CMNII 47352), ranging from length 25 mm, width 17 mm to length 28 mm, width 19 mm. All type material from the type locality.

Type locality: On lower beach flat at low tide, southern side of Bragman's Bluff (Station 1), approximately 2.5 km north of Puerto Cabezas, Miskito Coast, Nicaragua.

Distribution: At present, known only from the beach area near Bragman's Bluff, Puerto Cabezas, Nicaragua, but may possibly be found southward along the entire Miskito Coast.

Etymology: Named for the Miskito Indians.

Remarks: The finding of a Caribbean *Micromactra* species was one of the most interesting and important discoveries to be uncovered during my research in Nicaragua. Until now, the genus was known from the western Atlantic by only a single cooler-water species, the Brazilian Province *Micromactra janeirocnsis* (E.A. Smith, 1915), which ranges from Espirito Santo State, Brazil to Urnguay (Rios, 1975:236). On the other hand, the genus is well-represented in the Eastern Pacific, with at least five species occurring in the Panamic Province alone (Keen, 1971:204).

Of the known *Micromactra* species, both Eastern Pacific and western Atlantic, *M. miskito* most closely resembles the Pacific *M. californica* (Conrad, 1837) which ranges from the Puget Sound southward to Costa Rica, and they form another example of a previously-unknown Panamic-Caribbean sibling species pair. The new species differs from its Pacific analogue in being slightly more elongated with a noticeably more truncated posterior end, in having more prominent, more highly elevated umbones, and in having a slightly more concave lunular area. Otherwise, the two species are very similar, especially in having virtually identical patterns of umbonal undulations.

From the only other Atlantic *Micromactra* species, *M. janeirocnsis*, *M. miskito* can be separated by the following characters; *1. shell shape*—the new species has a

much more elongated, slender shell than does *M. janeiroensis,* and the posterior end of *M. lindae* is much more pointed and sharply-angled than the blunted, more rounded posterior of its southern congener; 2. *undulating sculpture*—the undulating, wavy sculpture pattern (the main characteristic of the genus *Micromactra*) is confined to the umbonal region of *M. miskito,* while on *M. janeiroensis* it extends onto the main shell body, often covering as much as two-thirds of the shell surface.

Petricolidae
Petricolinae
Petricola Lamarck, 1801
Petricolaria Stoliczka, 1870
Petricola (Petricolaria) donnae new species
(Figures 24, 25)

Description: Shell thin, fragile, small for subgenus (holotype length 28 mm), elongated, subcylindrical in shape, with dorsal and ventral margins roughly parallel. Umbones rounded, elevated above hinge line, placed far forward near anterior end. Small flattened lunule present just anterior to umbones. Anterior end pointed, posterior end wider and distinctly rounded. Shell exterior covered with numerous fine, closely-spaced radial ribs. Radial ribs, especially those on anterior one-fourth of shell, become coarser and farther apart toward anterior end of shell. Radial ribs crossed by numerous, evenly-spaced concentric ribs. Intersections of concentric ribs with large anterior radial ribs producing small spine-like scales on radial ribs. Umbones rounded, recurved, strongly prosogyrate. Hinge line straight, smooth. Hinge without lateral teeth. Cardinal teeth paired, typically petricolid, with anterior tooth curved and hooklike, and with posterior tooth flattened and bifurcated. Pallial line sinusoidal in form, with long, deep, pointed sublinguiform pallial sinus. Pallial sinus extends horizontally to shell midline. Shell exterior and interior pale cream-yellow, with posterior end stained pale orange. Pale orange color may be staining from the red clay within which the animal had bored, and not part of the actual shell color.

Type material: Holotype (pair) (CMNH 47373), length 28 mm, width 9 mm.

Type locality: On beach near clay cliffs, approximately 1 km north of main pier of Puerto Cabezas, Miskito Coast, Nicaragua.

Distribution: At present, known only from the clay cliff and clay reef areas near Puerto Cabezas, Nicaragua.

Etymology: Named for Mrs. Donna Villa, of Wellington, Florida. Her husband, Dr. Jaime Villa, collected the unique holotype and wished to have the species named for her.

Remarks: Prior to the discovery of *Petricola (Petricolaria) donnae,* the subgenus was known in the western Atlantic from only a single wide-ranging species, *P. (Petricolaria) pholadiformis* (Lamarck, 1818) (Figure 23). Although only a single specimen of the new species has been collected, the new *Petricolaria* is so different that there can be no doubt that it represents a previously-unknown and undescribed animal. The apparent rarity of the new species is most probably an artifact of collectibility. Judging from the abundance of bivalve borings in the clay reefs, the species is probably common, but is deeply buried below the surface and is virtually inaccessible. Rarely, specimens such as the holotype may wash out of broken clay blocks during storms.

The new species can be readily separated from its only western Atlantic congener in the following ways; *1. shell shape—Petricola donnae* is a much shorter, stockier species with a proportionally wider, less elongated shell; the posterior end of *P. donnae* is much wider and noticeably more rounded than the more pointed posterior end of *P. pholadiformis*; the umbones of *P. donnae* are also proportionally narrower and more acute than those of *P. pholadiformis,* and project farther above the hinge line; 2. *shell sculpture*—the posterior and central radial ribs of *P. donnae* are much more numerous and better-defined than those of *P. pholadiformis,* while the anterior radial ribs of *P. donnae* are not as large nor as heavily sculptured as those of *P. pholadiformis* (readily seen in a comparison of Figures 23 and 24).

Of the known American *Petricolaria* species, *P. donnae* is actually most similar morphologically to the Panamic Province *P. cognata* C.B. Adams, 1852, especially in overall shell shape and size. The Pacific *P. cognata,* however, has much coarser and more heavily-sculptured anterior radial ribs, much in the manner of *P. pholadiformis.* Even with this sculptural difference, *P. donnae* is still very similar to *P. cognata* and can be considered to be its Atlantic analogue, just as the Panamic *P. parallela* Pilsbry and Lowe, 1932 is the Pacific analogue of the Atlantic *P. pholadiformis.* Interestingly enough, the normally-common Caribbean clay-dwelling *P. pholadiformis* has not been reported from the Miskito Coast, where it appears to have been replaced by *P. donnae.*

BIOGEOGRAPHICAL IMPLICATIONS

Based upon the faunal evidence presented in this paper and in previous studies (Fluck, 1905–1906; Petuch, 1981,1987,1988), it is now known that the shoreline and estuarine areas of eastern Central America, from approximately Cabo Camaron, Honduras to near Bluefields, Nicaragua, house a combined molluscan fauna that bears only a partial relationship to the surrounding Caribbean Molluscan Province. Since this new faunal subdivision of the Caribbean Province is centered on the Miskito Coast of Honduras and Nicaragua, I here propose the name "Miskitia" for this newly-discovered biogeographical unit. At present, the biogeographical subdivisions of the Caribbean Province, particularly at the subprovincial level, are still virtually unknown, so I prefer to use "Miskitia" as an informal designation—simply to emphasize the atypical Caribbean nature of the nearshore molluscan fauna. As the area is better studied, it

may be proven that Miskitia actually represents a separate and discrete molluscan subprovince.

As presently understood, the tropical Americas contain two types of marine molluscan faunas; a "Caribbean"-type fauna and a "Panamic"-type fauna. A classic Caribbean fauna contains index genera such as *Lithopoma, Puperita, Smaragdia, Cenchritis, Chicoreus, Fasciolaria,* s.s., *Dolicholatirus, Conella, Cariboliva, Turbinella, Cordilyria, Lindapecten* ("*Acquipecten*" *muscosus* complex), *Spengleria,* and in some areas *Voluta* and *Siphocypraea.* A classic Panamic fauna, on the other hand, contains index genera such as *Ancistromesus, Trochita, Jenneria, Malea, Pseudozonaria, Muricanthus, Northia, Agaronia, Noetia* (s.s.), and *Micromactra.* These faunal characterizations were based on assessments of transisthmian assemblages (Caribbean and Eastern Pacific) and were reported on by Olsson (1972), Petuch (1982), Radwin (1969), Vermeij and Petuch (1986), and Woodring (1966). From the results of these studies, it was generally accepted that the Caribbean and Panamic molluscan faunas, with the exception of some analogue species ("cognates" of Radwin, 1969), were quite different-appearing, and that the Panamic fauna was much more diverse and species-rich (Olsson *in* Olsson & Petit,1964: 525). Subsequent works (Petuch, 1987;1988;1990), however, have shown that the Caribbean area, particularly northern South America and isolated islands, does harbor some previously-unrecognized "Panamic" ("paciphiles" of Woodring, 1973) genera such as *Cotonopsis, Truncaria, Agaronia, Aphera, Knefastia,* and *Cyclothyca,* as well as supposedly-extinct genera such as *Falsilyria, Conomitra, Plcioptygma, Cerithioclava,* and *Paraborsonia.* The Caribbean, then, can be seen to be far richer and more complicated, faunistically, than was previously thought.

With the present discovery of the new western Caribbean fauna reported here, the tropical Americas are now known to contain three "Panamic"-type faunas; an Atlantic component containing the Brazilian Province (as defined by Petuch, 1988:166; Harasewych, Petit & Verhecken, 1992) and the Miskitian area of the Caribbean Province, and a Pacific component containing the classic Panamic Province and offshore Cocos Island and Galapagos Islands "Subprovinces" (possibly full provinces). The biogeographical divisions that contain "Panamic"—type faunas and that show close faunal affinities to each other are shown in Figure 49, and as can be seen, Miskitia represents a shallow water Panamic fauna that has been left behind in the western Atlantic after the final closure of the Central American Isthmus in the late Pliocene. A short listing of shallow water and estuarine endemics and their living Panamic analogues (cognates) demonstrates the Panamic-Eastern Pacific nature of the Miskitian fauna:

Miskitia Restricted	**Panamic (Pacific)**
Strombus pugilis nicaraguensis	*S. gracilior*
Ficus villai	*F. ventricosa*
Agaronia hilli	*A. propatula*
Cancellaria mediamericana	*C. obesa*
Conus paschalli	*C. regularis*
Noetia lindae	*N. olssoni*
Pacipecten leucophaeus	*P. tumbezensis*
Plicatula miskito	*P. penicillata*
Micromactra miskito	*M. californica*
Polymesoda placans	*P. nicaraguana*
Petricola donnae	*P. cognata*

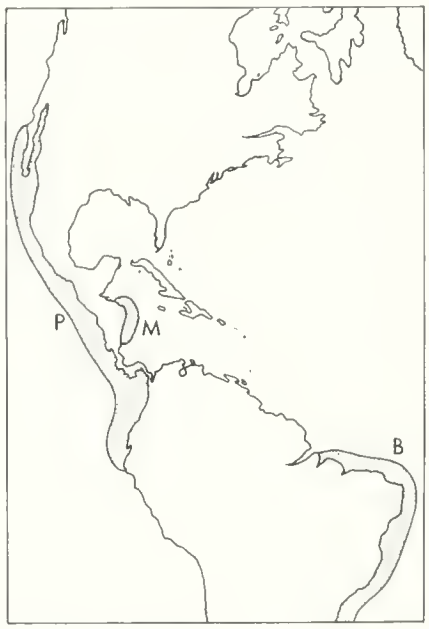


Figure 49. Molluscan biogeographical areas of the tropical Americas that show close faunal affinities, particularly in their shoreline assemblages. P = Panamic Molluscan Province; M = Miskitia (subprovince of the Caribbean Molluscan Province ?); B = Brazilian Molluscan Province. All three share genera such as *Agaronia, Noetia* (s.s.), and *Micromactra.* With the Panamic Province, Miskitia also shares species of the *Plicatula penicillata* complex, *Pacipecten,* and the *Petricola* (*Petricolaria*) *cognata* complex.

A close relationship to the other Atlantic "Panamic" fauna, the Brazilian Province, is also readily demonstrated by the following Miskitian endemics and their Brazilian analogues:

Miskitia Restricted	**Brazilian**
Strombus pugilis nicaraguensis	*S. pugilis worki*
Agaronia hilli	*A. travassosi*
Cancellaria mediamericana	*C. petuchi*
Conus paschalli	*C. tostesi*
Noetia lindae	*N. bisulcata*
Mactra inceri	*M. iheringi*
Micromactra miskito	*M. jancirocnsis*

All three "Panamic" faunas can be seen to share the genera *Agaronia, Noetia* (s.s.), and *Micromactra.* Interestingly enough, all three areas also have their own member of a *Strombus* (s.s.) species complex (*S. pugilis nicaraguensis* Fluck, 1905, *S. pugilis worki* Petuch,

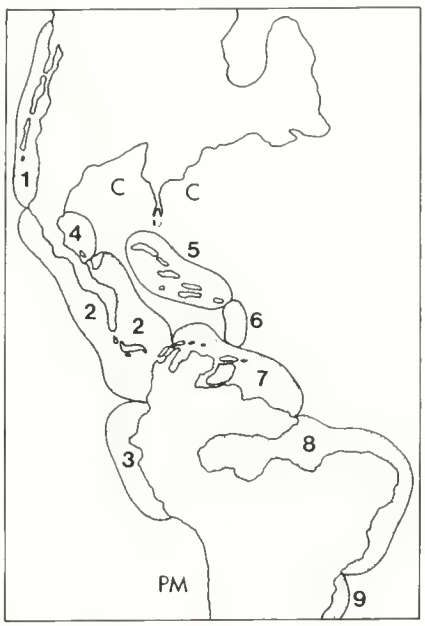


Figure 50. Configurations of the American tropical seas during the early Piacenzian Pliocene, showing the distributions of the subprovinces of the Gatunian Molluscan Province (shaded areas) (taken from Petuch, 1988). 1 = Imperialian Subprovince, 2 = Limonian Subprovince, 3 = Esmeraldan Subprovince, 4 = Agueguexitean Subprovince, 5 = Guraban Subprovince, 6 = Carriacouan Subprovince, 7 = Puntagavilanian Subprovince, 8 = Piraban Subprovince, 9 = Camachoan Subprovince. C = region of the Caloosahatchian Molluscan Province (with four subprovinces; see Petuch, 1997); PM = region of the Protomagellanic Molluscan Province.

1993, and *S. gracilior* Sowerby, 1825), a *Cancellaria* (s.s.) species complex (*C. mediamericana* n.sp., *C. petuchi* Harasewych, Petit & Verhecken, 1992, and *C. obesa* Sowerby, 1832), and *Conus* (*Leptoconus*) species complex (*C. paschalli* n.sp., *C. tostesi* Petuch, 1986, and *C. regularis* Sowerby, 1833).

The shared genera and species complexes of the geographically-separated Panamic and Brazilian Provinces and Miskitia reflect a common origin in the Gatunian Province (Petuch, 1982) (Figure 50) during the late Pliocene, prior to the formation of the Panamanian Isthmus and Amazon River barriers. Since the final closing of Panama (Whitmore & Stewart, 1965:185), the Panamic Province has retained a nearly intact Gatunian appearance (Vermeij & Petuch, 1986) while the Caribbean Province has become a mixture of Gatunian survivors and immigrants from the northern Caloosahatchian Province (Petuch, 1988:115–116; 1997). Prior to the discovery of Miskitia, the only Atlantic area that retained any semblance of the Gatunian Province (Piraban Subprovince) was the Brazilian Province, which shares with the post-closure Panamic Province additional genera such as *Malea*, *Northia*, and *Pleuroploca* (s.s.). Miskitia, then, represents yet another pocket of shallow water Gatunian survivors within the western Atlantic, and one that is contiguous with typical Caribbean assemblages to the north and south.

The ancestral fauna of Miskitia is found within the fossil beds of the Limonian Subprovince of the Gatunian Province (Figure 50), a Pliocene biogeographical area that spanned both sides of the then-open Central American Isthmus. A survey of the eastern Costa Rican Limón and Gatun Formations and western Costa Rican Armuelles and Charco Azul Formations (listed by Olsson, 1922; 1942), which all contain typical Limonian Gatunian elements, will readily demonstrate the Gatunian ancestry of the Recent Miskitian fauna. As in the cases of the Recent Brazilian and Panamic Provinces, Miskitia also contains analogues with the older Limonian Subprovince. These include:

Miskitian Restricted	**Limonian**
Strombus pugilis nicaraguensis	*S. pugiloides*
Ficus villai	*F. carbasea*
Agaronia hilli	*A. costaricensis*
Cancellaria mediamericana	*C. barretti*
Conus paschalli	*C. costaricensis*
Noctia lindae	*N. subreversa*
Pacipecten leucophaeus	*P. costaricensis*
Micromactra miskito	*M.* sp. (Armuelles Form., Olsson, 1942)

These Limonian paleoanalogues appear to be the direct ancestors of the Miskitian species.

The survival of a "Panamic", Gatunian-derived Miskitian fauna in the Caribbean region is also probably due to the retention of a Panamic-type coastal habitat within the western Atlantic. Both the Pacific and Atlantic coasts of Honduras and Nicaragua are typified by siliciclastic, muddy, terrigenous run-off, high productivity environments and both coasts have large mangrove forests with extensive estuarine areas. Although this type of coastline is typical of the Panamic Province south of Mexico, it occurs only sporadically within the Caribbean Basin, where carbonate environments predominate. To the north of Miskitia, the extensive coral reef systems of the Great Barrier Reef of Belize and the Bay Islands of Honduras predominate. To the south, the open, clean sand coasts and coral reef systems of Costa Rica, Panama, and the San Blas Islands (the Blasian Subregion of Petuch, 1990) represent a mirror image of the carbonate environments of the Bay Islands. The Miskitian area, environmentally and sedimentologically, represents an "island" of muddy nearshore habitats wedged between these two extensive coral-dominated subregions. This siliciclastic-dominated environment may have been present since before the closure of Panama, allowing the older Gatunian elements to survive within the Caribbean Sea even though their congeners died-out in the other Atlantic Gatunian subprovinces due to lowered productivity and increased carbonate build-up (Vermeij & Petuch, 1986).

The discovery of Miskitia further underscores the faunal and temporal heterogeneity of the Caribbean Molluscan Province and, hopefully, will focus the attention

of biogeographers on one of the most biotically complicated, but yet unexplored, areas of the entire Atlantic Ocean.

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The Protoconch of *Fastigiella carinata* Reeve, 1848 (Mollusca: Cerithiidae)

Jesús Ortea
Laboratorio de Zoología
Facultad de Biología
Universidad de Oviedo
33005 Oviedo, Asturias SPAIN

José Espinosa
Istituto de Oceanología
Avenida Primera 18406 entre 184 y 186
Playa, 12100, Havana CUBA

Houbrick, Robertson and Abbott (1987) provided a detailed description of the shell, operculum, radula and anatomy of *Fastigiella carinata* Reeve, 1848, and confirmed the taxonomic position of this previously enigmatic species in the family Cerithiidae. These authors also provided information about the ecology and geographic distribution of this species, which is restricted to the Great Bahamas Bank and the northwestern coast of Cuba. The specimens described and figured by Houbrick *et al.* (1987) lacked not only the protoconch, but also the first teleoconch whorl. The purpose of this short note is to describe and illustrate the protoconch of *Fastigiella carinata* Reeve, 1848.

Young specimens of *F. carinata* were collected at several localities along the northern coast of Cuba. Voucher specimens are deposited in the Instituto de Oceanología and Instituto de Ecología y Sistemática, in Havana.

The protoconch (Figures 1–2) is white, nearly cylindrical, composed of two whorls, and has a height of 590 µm. Pronounced axial costae are evident within the first quarter whorl, but disappear after ½ whorl. Three to four spiral cords appear between the first ¼ and ½ whorl, becoming well-developed after ½ whorl. Beginning at ½ whorl, small axial plicae appear normal to the suture, but do not reach the first spiral cord. The transition to the teleoconch is abrupt and marked by the loss of these axial plicae.

Protoconchs of *F. carinata* are common in the sand at some localities along northern Cuba (eg. Jibacoa Beach) (E. Rolán, personal communication). This leads us to conjecture that this species has lecithotrophic development with a brief planktonic phase and a high mortality at metamorphosis. This may contribute to the limited geographic distribution of this taxon.

ACKNOWLEDGEMENTS

Special thanks to Dr. Emilio Rolán for providing information and the Scanning Electron Micrographs.

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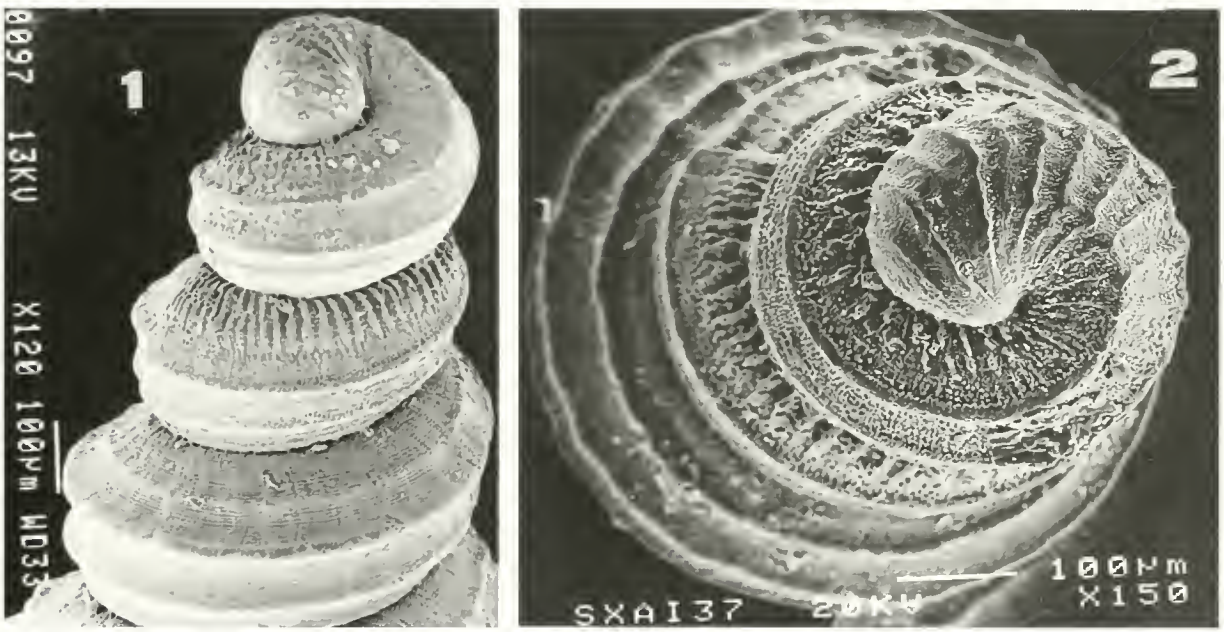

Figures 1–2. Protoconch of *Fastigiella carinata*. **1.** Lateral view, specimen from Esquival Key, Sagua la Grande, Cuba. Scale bar = 100 µm. **2.** Apical view, specimen from Jibacoa Beach, Havana, Cuba. Scale bar = 100 µm.

Notices

THE R. T. ABBOTT VISITING CURATORSHIP

The Bailey-Matthews Shell Museum is pleased to invite applications for the 1998 R. T. Abbott Visiting Curatorship.

The Curatorship, established originally in accordance with the wishes of the late Dr. R. Tucker Abbott, Founding Director of Shell Museum, is awarded annually to enable systematic malacologists to visit the museum for a period of one to two weeks. Abbott Fellows will be expected, by performing collection-based research, to assist with the curation of the portions of the museum's Mollusk Collection and to provide one evening talk for the general public. The museum collection consists of marine, freshwater, and land shells, with emphasis on SW Florida. A large percentage of the records has been catalogued through a computerized database management system. A substantial portion of the time will be available for research in the museum collection, but field work in SW Florida can be arranged. The R. T. Abbott Visiting Curatorship is accompanied by a stipend of $1,500.

Interested malacologists are invited to send a copy of their curriculum vitae together with a letter detailing their areas of taxonomic expertise and research objectives, and to provide a tentative title for their talk. Send materials to:

Dr. José H. Leal, Director
The Bailey-Matthews Shell Museum
P.O. Box 1580
Sanibel, FL 33957

Applications for the 1998 Visiting Curatorship should be sent no later than January 31, 1998. The award will be announced by February 28, 1998. Questions about the R. T. Abbott Visiting Curatorship should be directed to Dr. Leal at:

(941) 395-2233; fax (941) 395-6706, or e-mail: leal@water.net

In Memoriam

Donald Richard Moore

1921–1997

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THE NAUTILUS publishes papers on all aspects of the biology and systematics of mollusks. Manuscripts describing original, unpublished research as well as review articles will be considered. Brief articles, not exceeding 1000 words, will be published as notes and do not require an abstract. Notices of meetings and other items of interest to malacologists will appear in a news and notices section.

Manuscripts: Each original manuscript and accompanying illustrations should be submitted in triplicate. Text must be typed on one side of 8½ × 11 inch white paper, double spaced throughout (including literature cited, tables and figure captions), with at least 1 inch of margin on all sides. All pages must be numbered consecutively. If printed on a word processor, the right margin should be ragged rather than justified. Authors should follow the recommendations of the *Council of Biology Editors Style Manual,* which is available from the Council of Biology Editors, Inc., 60 Revere Dr., Suite 500, Northbrook, IL 60062, USA (http://www.cbe.org/cbe). The first mention of a scientific name in the text should be accompanied by the taxonomic authority, including year. Latin names and words to be printed in italics must be underlined; leave other indications to the editor. Metric and Celsius units are to be used.

The sequence of sections should be: title page, abstract page, introduction, materials and methods, results, discussion, acknowledgments, literature cited, tables, figure captions, figures. The title page should include the title, author's name(s) and address(es). The abstract page should contain the title and abstract, which should summarize in 250 words or less the scope, main results and conclusions of the paper. The abstract may be followed by a maximum of 8 key words. All references cited in the text must appear in the literature cited section and vice versa. In the literature cited section, all authors must be fully identified and listed alphabetically. Follow a recent issue of THE NAUTILUS for bibliographic style, noting that journal titles must be unabbreviated. Information on plates and figures should be cited only if not included in the pagination. Tables must be numbered and each placed on a separate sheet. A brief legend must accompany each table. Captions for each group of illustrations should be typed on a separate sheet and include a key to all lettered labeling appearing in that group of illustrations.

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Department of Geology
University of California at Davis
Davis, CA 95616

Dr. G. Thomas Watters
Aquatic Ecology Laboratory
1314 Kinnear Road
Columbus, OH 43212-1194

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Two New Deep-Water Pseudolividae (Neogastropoda) from the South-West Pacific

Philippe Bouchet
Muséum national d'Histoire naturelle
55 rue Buffon, 75005 Paris FRANCE
E-mail: bouchet@cimrs1.mnhn.fr

Geerat J. Vermeij
Department of Geology and Center
for Population Biology
University of California at Davis
Davis, CA 95616 USA
E-mail: vermeij@geology.ucdavis.edu

ABSTRACT

The new genus *Fusulculus*, conchologically most similar to *Benthobia* Dall, 1889 and *Zemira* H. & A. Adams, 1853, is erected for axially sculptured species of Pseudolividae with shouldered whorls and obsolete labral tooth; the columellar and parietal callus is of very limited extent, and a parietal rib at the adapical end of the inner lip is absent. Two new species, *Fusulculus crenatus* (type of genus) and *F. albus* are described from bathyal (400–800 m) hard bottoms at tropical and subtropical latitudes in the southwest Pacific. No post-Paleocene species of Pseudolividae are known from the tropical Indo-Pacific; the habitat of *Fusulculus* is bathymetrically transitional between those of *Benthobia*, from abyssal depths, and the various genera from subtidal waters in southern Australia, South Africa and Angola.

Key words: Muricoidea, Pseudolividae, *Fusulculus*, labral tooth, deep-sea, New Caledonia, New Zealand.

INTRODUCTION

Among the many remarkable mollusks in the deep-water fauna around New Caledonia are two species that belong to a previously unknown genus of the neogastropod family Pseudolividae. The discovery of these species documents the occurrence of the Pseudolividae at tropical latitudes in the Indo-West-Pacific region, whose enormous molluscan fauna is otherwise wholly lacking in members of this relict family. Here we introduce the new genus *Fusulculus* and describe the two new species belonging to it.

ABBREVIATIONS USED

LACM	Los Angeles County Museum of Natural History, Los Angeles
MNHN	Muséum national d'Histoire naturelle, Paris
NM	Natal Museum, Pietermaritzburg
NMNZ	Museum of New Zealand Te Papa Tongarewa, Wellington
NZOI	National Institute of Water and Atmospheric Research [formerly New Zealand Oceanographic Institute], Wellington
dd	empty shell
lv	collected alive.

Superorder CAENOGASTROPODA Cox, 1960
Order NEOGASTROPODA Wenz, 1938
Superfamily Muricoidea Rafinesque, 1815
Family Pseudolividae Fischer, 1884

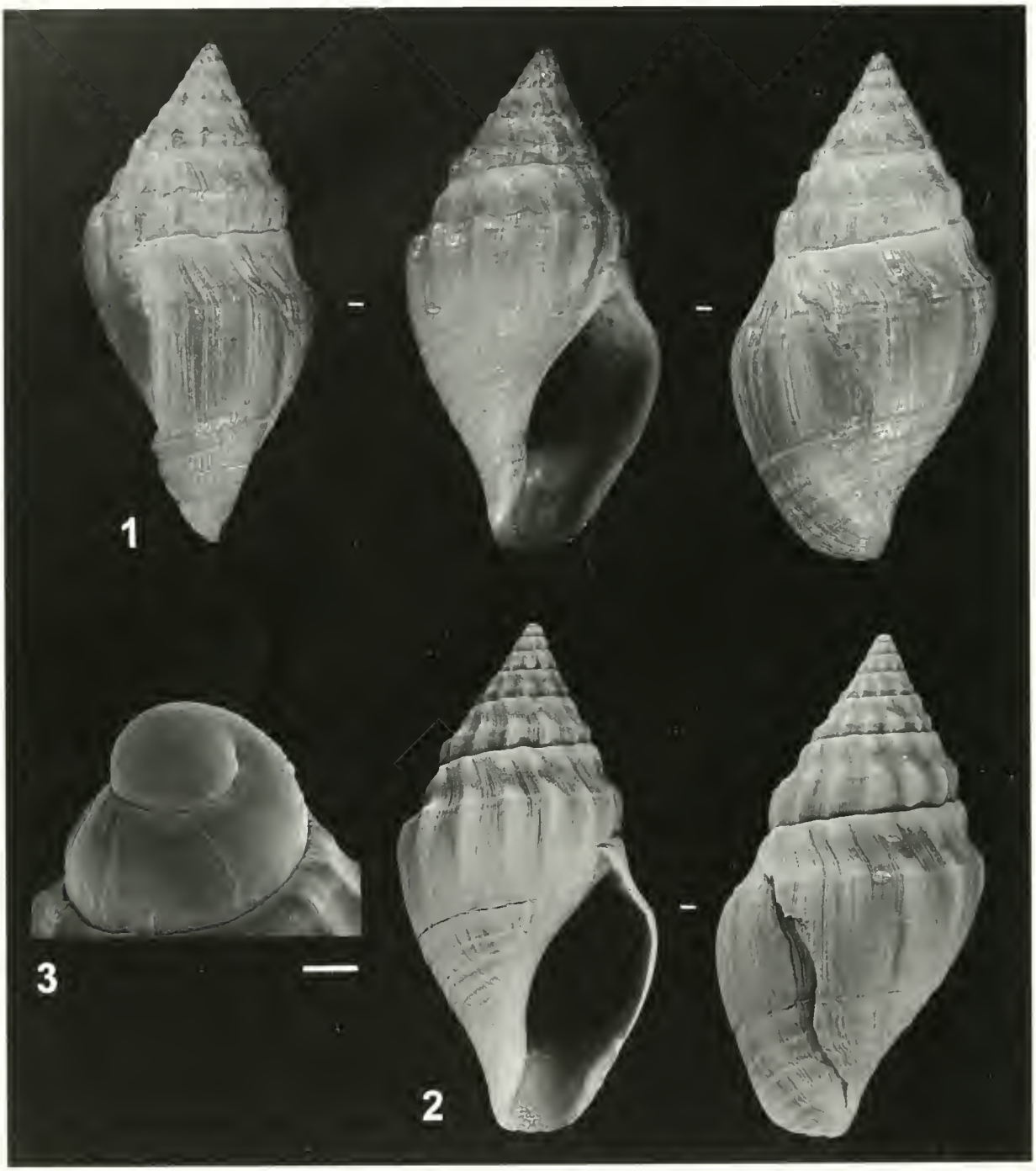
Genus *Fusulculus* new genus

Type species: *Fusulculus crenatus* new species

Description: Small pseudolivid with relatively high-spired, fusiform shell in which the spire comprises 33 to 39% of total shell height; shell consisting of one protoconch whorl [in species with non-planktotrophic development] and three to six teleoconch whorls; teleoconch whorls separated by impressed sutures; base of last whorl constricted above short siphonal canal; sculpture of last whorl consisting of axial riblets on adapical part of whorl, crossing finer spiral cords; conspicuous spiral groove below middle of last whorl, ending in very small labral tooth at edge of outer lip; below the groove, surface adorned with stronger spiral cords; inner side of outer lip smooth; anterior siphonal notch very shallow; fasciole, umbilical slit, and parietal rib absent; columellar callus of very limited extent, thin; adapical end of outer lip with obsolete notch. Operculum lanceolate, nucleus terminal. Radula with broad, slightly concavely arched rachidian, with three strong medially placed cusps, central one stronger; lateral teeth with strong, solid base, and short, claw-like cusp.

Etymology: Combination of *fusus* (Latin: spindle) and *sulculus* (Latin: small groove).

Remarks: *Fusulculus* belongs to a group of Pseudolividae in which the columellar and parietal callus is of very limited extent, and in which a parietal rib at the adapical end of the inner lip is absent. Among Recent genera, *Fusulculus* is most similar to *Benthobia* Dall,



Figures 1–3. *Fusulculus crenatus* new genus, new species, New Hebrides Arc, 22°17'S, 171°18'E, 450–550 m. **1–2.** Holotype, height 16.5 mm; **1.** Natural view; **2.** Coated to enhance sculpture. **3.** Protoconch, scale bar = 200 μm.

1889 (type species: *B. tryonii* Dall, 1889) and *Zemira* H. & A. Adams, 1853 (type species: *Eburna australis* G. B. Sowerby I, 1833). All three genera are characterized by a very shallow siphonal notch, a spiral external groove that is situated just below the middle of the last whorl, by having the inner side of the outer lip smooth, and by lacking a fasciolar ridge bordering the anterior notch. Axial riblets confined to the subsutural ramp and shoulder are characteristic of *Fusulculus* as well as of *Benthobia* and of the Late Oligocene Australian species *Zemira tessellata* Tate, 1894 (see Ponder & Darragh, 1975; Bouchet & Warén, 1985). *Fusulculus* further resembles *Benthobia* in having the labral tooth obsolete, and by being basally slightly constricted; but it differs from *Benthobia* by having shouldered instead of evenly rounded whorls, by having a higher spire (spire comprising 33 to

39% instead of 25% of shell height), and a much less inflated and more elongate last whorl, and by having fine instead of obsolete spiral sculpture. *Fusulculus* resembles *Zemira* in having a moderately high spire (spire about 33% of total shell height in *Z. australis*) and in possessing fine spiral sculpture; but it differs in having the last whorl basally constricted instead of convex-sided and conical, by having appressed instead of deeply channeled sutures, and in having an obsolete instead of prominent and sharp labral tooth. Most species of *Zemira*, moreover, lack axial sculpture.

In Recent faunas, two other genera with limited callus development and without a parietal rib are *Luizia* Douvillé, 1934 (type species: *Buccinum (Luizia) costae* Douvillé, 1934; Miocene, Angola) and *Naudoliva* Kilburn, 1989 (type species: *N. caitlinae* Kilburn, 1989; southeastern Africa). *Luizia* resembles *Fusulculus* in having axial riblets on the upper part of the whorls, by having appressed sutures, and by the relatively high position of the groove on the last whorl; but it differs from *Fusulculus* in usually being lower-spired (spire comprising 20% of shell height in *L. zebrina* (A. Adams, 1855) from Angola, instead of 33 to 39%), in having the inner side of the outer lip finely lirate instead of smooth, by having a distinct labral spine, and in lacking the basal constriction of the last whorl. *Naudoliva*, like *Fusulculus*, is relatively high-spired (spire comprising 36% of total shell height) and basally constricted, and the inner side of its outer lip is likewise smooth; but it differs from *Fusulculus* in having a long labral spine, which is situated at the end of a slightly raised spiral band near the base of the shell rather than at the end of a groove that is situated at a high position on the whorl. *Naudoliva*, moreover, has a siphonal fasciole, which is lacking in *Fusulculus*.

The Late Cretaceous to Late Eocene genus *Calorebama* Squires, 1989 (type species: *Pseudoliva dilleri* Dickerson, 1914; California) is characterized by a broadly fusiform shell with a moderately low spire (spire comprising less than 27% of total shell height), eight to twelve axial folds often raised as nodes at the shoulder or periphery, and fine spiral sculpture over the whole whorl surface, as well as by the absence of a parietal thickening and of outer-lip lirae. As in *Fusulculus*, the spiral groove is located at a relatively high position on the whorl. *Calorebama* differs from *Fusulculus* by its lower spire, and by having a conical or evenly convex last whorl instead of a basally constricted body whorl. The axial sculpture of *Fusulculus* is finer.

Fusulculus crenatus new species
(Figures 1–4, 6)

Type material: Holotype (dd) in MNHN; paratypes in NMNZ (1 dd), NM (1 dd), LACM (1 dd) and MNHN (2 lv, 7 dd).

Type locality: New Hebrides Arc, 22°17'S, 171°18'E, 450–550 m [VOLSMAR sta. DW30].

Material examined: Coral Sea. MUSORSTOM 5: sta. 313, 22°24'S, 159°33'E, 780–930 m, 4 dd.—Loyalty Basin. BIOGEOCAL: sta. DW289, 20°36'S, 167°00'E, 830–840 m, 3 dd.—New Hebrides Arc. VOLSMAR: sta. DW30, 22°17'S, 171°18'E, 450–550 m, 2 lv, 11 dd (type material).—Wallis & Futuna. MUSORSTOM 7: sta. DW540, 12°27'S, 177°28'W, 600 m, 1 lv, 12 dd.; Sta. DW578, 13°08'S, 176°16'W, 640–730 m, 2 dd.; Sta. DW586, 13°11'S, 176°13'W, 510–600 m, 2 dd (all MNHN).

Distribution: SW Pacific, from the Coral Sea to NE of Fiji, alive in 550–600 m, shells to 830 m.

Description: Shell thick, solid, ovoid, consisting of 0.9 protoconch and 5.7 teleoconch whorls, protoconch with smooth glassy shell, teleoconch more chalky, with thin and fragile intritacalx and strong incremental lines, most distinct in lower parts of shell surface between ribs. Teleoconch whorls convex with a distinctly concave subsutural ramp occupying about 2/3 of exposed height of spire whorls. Sculpture consisting of strong axial ribs, 14 per whorl, and weaker spiral cords; one adapical cord just adjacent to suture, no cord but only very indistinct spiral threads in subsutural ramp, 2 cords below ramp (5 on penultimate whorl), forming prominent nodules at intersection with ribs. Last whorl with ca. 10 cords adapically of groove, those on shoulder stronger, 6 abapically with interspaces broader than cords; groove narrow and sharp, terminating in a short, pointed triangular tooth at aperture; axial ribs not extending abapically of groove. Aperture ovate with broadly open siphonal notch, columella simple; outer lip not thickened, regularly convex except for constriction at level of subsutural ramp. Color salmon brown with whitish intritacalx on very fresh shells, fading in dead collected specimens. Operculum (figure 6) lanceolate, nucleus terminal. Radula (figure 4) with broad, slightly concavely arched rachidian, with three strong medially placed cusps, central one stronger; lateral teeth with strong, solid base, and short, claw-like cusp.

Dimensions: Holotype height 16.5 mm, diameter 7.9 mm, aperture length 10.4 mm, aperture width 4.0 mm. Largest specimen, height 18.4 mm.

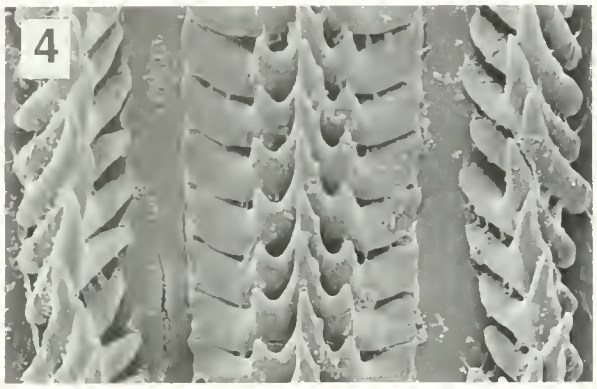
Remarks: A comparison with *F. albus* is given under the latter species.

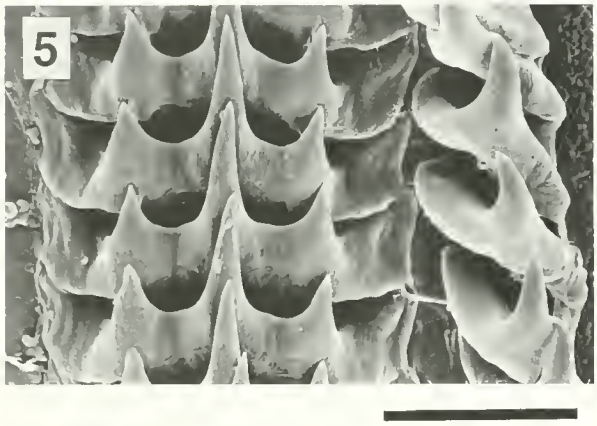
Fusulculus albus new species
(Figures 5, 7, 8–14)

Type material: Holotype (dd) in MNHN; paratypes in NMNZ (1 dd), NM (1 dd), LACM (1 dd) and MNHN (3 lv, 15 dd).

Type locality: North of New Caledonia, 18°42'S, 163°13'E, 668 m [MUSORSTOM 4 sta. DW160].

Material examined: New Caledonia (all MNHN). MUSORSTOM 4: sta. DW160, 18°42'S, 163°13'E, 668 m, 3 lv, 19 dd (type material).; BIOCAL: sta. DW48,





Figures 4–5. Radulae of *Fusuleulus* species. **4.** *Fusuleulus crenatus* new species, taken from paratype from type locality, scale bar = 50 μm. **5.** *Fusuleulus albus* new species, taken from paratype from type locality, scale bar = 20 μm.

Figures 6–7. Opercula of *Fusuleulus* species. **6.** *Fusuleulus crenatus* new species, from paratype from type locality, length 6.5 mm. **7.** *Fusuleulus albus* new species, taken from paratype from type locality, length 2.85 mm.

23°00'S, 167°29'E, 775 m, 2 dd.; BATHUS 4: sta. DW917, 18°47'S, 163°14'E, 397–400 m, 5 dd.—New Zealand. Three Kings Rise. R.V. Acheron, sta. BS391, 34°01'S, 172°07'E, 622 m, 7 dd (NMNZ M34932).; R.V. Tangaroa, sta. BS633, 34°20'S, 171°48'E, 440 m, 4 dd (NMNZ M100323).; Sta. BS634, 34°18'S, 171°45'E, 427 m, 2 dd (NMNZ M100322).; Sta. BS896, 34°01'S, 171°45'E, 201–216 m, 1 dd, 1 fragm. (NMNZ M100324).; Sta. BS898, 34°01'S, 171°44'E, 206–211 m, 1 dd (NMNZ M100321).; NZOI sta. U602, 31°31'S, 172°50'E, 1216–1385 m, 1 dd (NZOI).

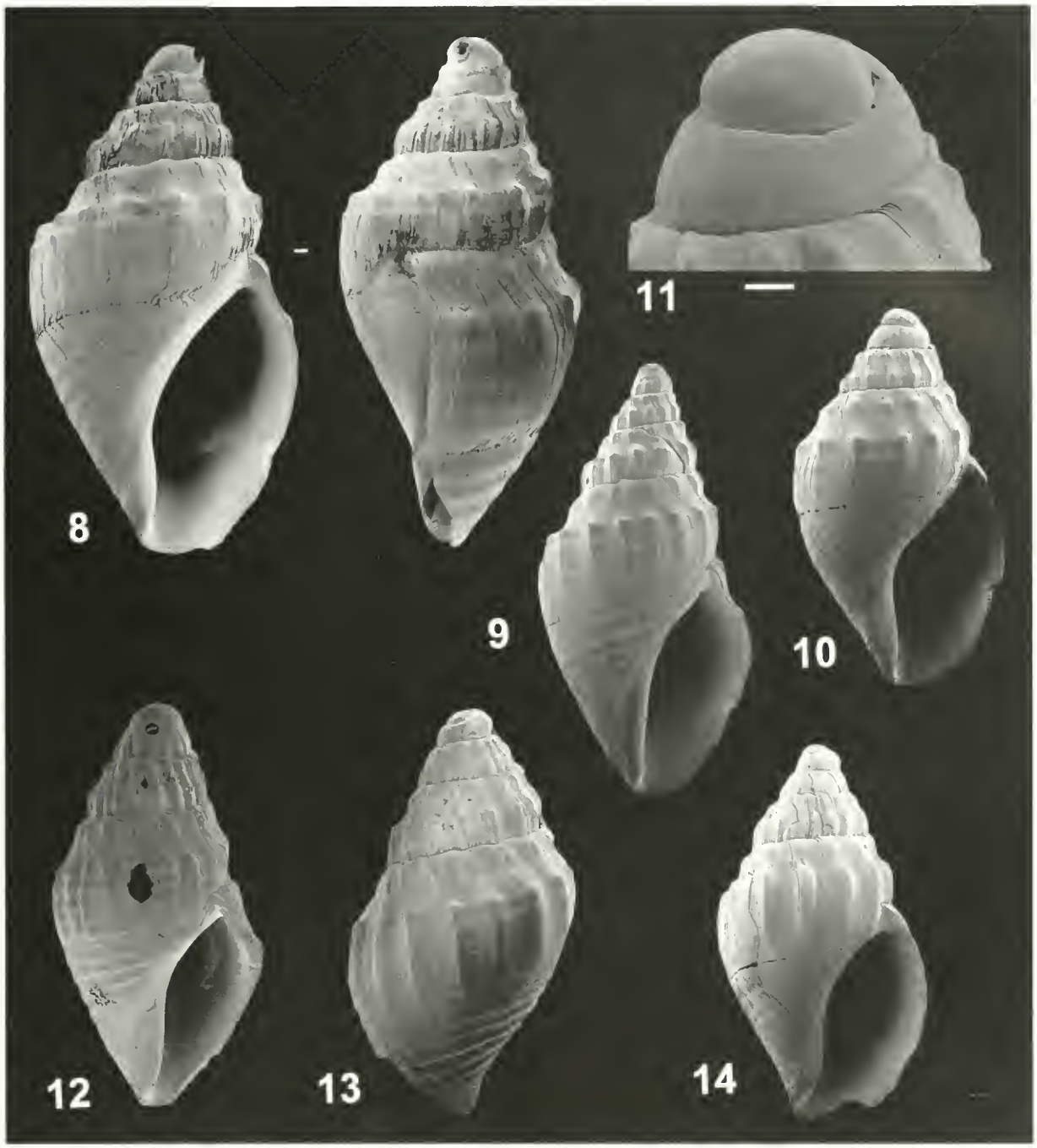
Distribution: New Caledonia, alive in 668 m, shells in 400–775 m; north of New Zealand, Three Kings Rise, shells in 211–622 m, with a single shell, probably transported vertically, in 1216–1385 m.

Description: Shell thick, solid, ovoid, consisting of 0.8 protoconch and 3.2 teleoconch whorls, protoconch with smooth glassy shell, teleoconch more chalky, with thin and fragile intritacalx and strong incremental lines, most distinct in lower parts of shell surface between ribs. Teleoconch whorls convex with a distinctly concave subsutural ramp occupying nearly half of exposed height of spire whorls. Sculpture consisting of low, broad axial ribs and low spiral cords, indistinct except at their intersection with ribs; one adapical cord just adjacent to suture, no cord in subsutural ramp, 3 cords below ramp, most adapical one forming prominent nodules at intersection with ribs, most abapical one very indistinct. Last whorl with 4 cords adapically of groove, 5 abapically; groove very sharp, terminating in a pointed triangular tooth at aperture; axial ribs not extending abapically of groove. Aperture ovate with broadly open siphonal notch, columella simple; outer lip not thickened, regularly convex except for a slight constriction at level of subsutural ramp and at level of groove. Color white. Operculum (figure 7) and radula (figure 5) as in *F. crenatus*.

Dimensions: Holotype height 7.9 mm, diameter 4.0 mm, aperture length 4.8 mm, aperture width 2.15 mm. Largest specimen [BATHUS 4 sta. DW917], height 10.3 mm.

Remarks: *Fusuleulus albus* differs from *F. crenatus* by having a smaller adult size, by being white instead of salmon brown in colour, and by having the axial riblets mainly confined to the shoulder area instead of extending from the suture to the groove. *Fusuleulus albus* is in these respects more like *Benthobia* than is *F. crenatus*. The two species co-occur in the New Caledonia region, but are never syntopic, nor sympatric.

The material from Three Kings Rise all consists of empty, sometimes worn or fragmentary shells. General shell morphology and proportions are similar to the material from New Caledonia. Most specimens have broadly spaced axial ribs and only weak spiral cords adapically of the spiral groove, thus the shoulder is not muricated as in the New Caledonia specimens (figure 1-1). One sample differs by having more numerous axial



Figures 8–14. *Fusulculus albus* new species. **8.** Holotype, height 7.9 mm, north of New Caledonia, 18°42'S, 163°13'E, 668 m. **9.** High-spired specimen, height 10.3 mm, north of New Caledonia, 18°47'S, 163°14'E, 397–400 m. **10–11.** Low-spired specimen, height 6.2 mm, south of New Caledonia, 23°00'S, 167°29'E, 775 m; **11.** Protoconch, scale line = 200 µm. **12–13.** Specimens from Three Kings Rise, height 6.5 and 5.9 mm respectively, north of New Zealand, 622 m (NMNZ M34932). **14.** Specimen with weak spiral sculpture, height 7.1 mm, North of New Zealand, 440 m (NMNZ M1100323).

ribs and strong spiral sculpture, extending adapically of the spiral groove (figures 12–13). Despite these differences, we interpret the New Caledonia and New Zealand material as probably representing a single species with discontinuous distribution along the Norfolk Ridge.

BIOGEOGRAPHICAL REMARKS

The family Pseudolividae was distributed nearly worldwide during the Late Cretaceous and Paleogene, but it has become progressively biogeographically restricted during the Neogene. In Recent seas, the family is rep-

resented in abyssal and bathyal waters by *Benthobia*, which is known from the deep Atlantic, Indian Ocean, and New Zealand (see Bouchet & Warén, 1985; Kantor, 1991). Shallower-water genera are known from New Caledonia (*Fusulculus*), temperate Australia (*Zemira*), warm-temperate southeastern Africa (*Naudoliva*), temperate and tropical western Africa (*Pseudoliva* Swainson, 1840; *Fulmentum* Fischer, 1884; *Luizia*), and western warm-temperate North America (*Macron* H. & A. Adams, 1853) and the Panamic Province (*Triumphis* Gray, 1857) (see Vermeij, 1998). During Miocene and Pliocene time, the family was also represented in temperate western South America by *Testallium* Vermeij and DeVries, 1997.

Beside the abyssal species of *Benthobia*, *Fusulculus* is the only genus of Pseudolividae known from moderately shallow water in the vast Indo-West Pacific region since Paleocene time. The family disappeared from Europe and Japan after the Late Eocene.

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Generic Revision of the Neogastropod Family Pseudolividae

Geerat J. Vermeij
Department of Geology and Center
for Population Biology
University of California at Davis
Davis, CA 95616 USA
vermeij@geology.ucdavis.edu

ABSTRACT

The neogastropod family Pseudolividae Cossmann, 1901, is a Late Cretaceous to Recent group of about one hundred species characterized by a spiral groove (pseudolivid groove) on the lower half of the last whorl, a labral tooth on the outer lip at the end of this groove, a posterior notch at the adapical end of the outer lip, spiral sculpture increasing in prominence toward the base, and an indeterminate, sharp-edged, planar outer lip. A genus-level revision based on shell characters supports previous anatomical studies in recognizing the Pseudolividae as a taxon distinct from other neogastropod families.

I recognize fourteen genera in the Pseudolividae: *Benthobia* Dall, 1889 (Recent, low-latitude bathyal and abyssal oceans); *Fulmentum* Fischer, 1884 (Recent, West and South Africa); *Fusopsis* Ravn, 1939 (Paleocene, Denmark); *Fusuleulus* Bouchet & Vermeij, 1997 (Recent, New Caledonia); *Hubachia* Etayo Serna, 1979 (Paleocene, Colombia); *Luizia* Douvillé, 1933 (Early Miocene to Recent, West Africa); *Macron* H. & A. Adams, 1853 (Early Miocene to Recent, warm-temperate North Pacific and Caribbean); *Naudoliva* Kilburn, 1989 (Recent, southeastern Africa); *Pseudoliva* Swainson, 1840 (Early Miocene to Recent, West Africa); *Sulcobuccinum* d'Orbigny, 1850 (Late Cretaceous (Campanian) to Early Oligocene, warm seas worldwide); *Sulcoliva*, new genus (type species: *Pseudoliva monilis* Olsson, 1928; Eocene, Peru); *Testallium* Vermeij & DeVries, 1997 (Early Miocene to Late Pliocene, western South America); *Triumphis* Gray, 1857 (Early Miocene?, Recent, tropical eastern Pacific); and *Zemira* H. & A. Adams, 1853 (Late Eocene to Recent, Australia). I designate *Buccinum fissuratum* Deshayes, 1835, the type species of *Sulcobuccinum*, of which the following taxa are subjective junior synonyms: *Buccinorbis* Conrad, 1865; *Calorebama* Squires, 1989; *Pegocomptus* Zinsmeister, 1983; and *Popenoeum* Squires, Zinsmeister & Paredes-Mejia, 1989. The genus *Sylvanocochlis* Melvill, 1903, is a junior subjective synonym of *Fulmentum*. *Pseudoliva guppyi* Mansfield, 1925, from the Late Miocene of Trinidad, is assigned to *Fusuleulus* with great hesitation. I propose *Sulcobuccinum multinodulosum* as a replacement name for *Pseudoliva chavani* Glibert, 1973, *non* Tessier, 1952. *Macron mcleani* is a new species described from the Recent fauna of the Gulf of California.

Genera removed from Pseudolividae include *Austrosphaera* Camacho *in* Furque & Camacho, 1949 (Late Cretaceous to Paleocene, Argentina); *Seymourosphaera* Oleinik & Zinsmeister, 1996 (Early Paleocene, Seymour Island, Antarctic Peninsula); and the Late Cretaceous genera *Fulgerca* Stephenson, 1941, *Hydrotribulus* Wade, 1916, and *Ptychosyca* Gabb, 1877, all from the Gulf Coastal Plain of the United States. These taxa are not reassigned to other families, but belong to basal buccinoids. *Nicema* Woodring, 1964, which has sometimes been considered a subgenus of *Triumphis*, is a Late Miocene to Recent tropical American genus here assigned to the buccinid subfamily Photinae. The Pliocene to Recent South African genus *Melapium* H. & A. Adams, 1853, may belong to the largely Paleogene family Strepturidae.

Key words: Muricoidea, Psuedolividae.

INTRODUCTION

The Pseudolividae is a distinctive family of some one hundred species of neogastropods, whose origin can be traced to the Late Cretaceous. The history of this family contrasts markedly with that of many other neogastropod families including the Muricidae, Fasciolariidae, Cancellariidae, Mitridae, and Conidae, which likewise originated during Late Cretaceous times (Taylor et al., 1980; Bandel, 1993). Whereas these latter families underwent spectacular phases of diversification during both the Paleogene and Neogene, the Pseudolividae have declined in diversity and geographical range since their peak during the Paleogene. The group is represented today by only about sixteen species, a number that is one to two orders of magnitude smaller than the living diversity in each of the other families.

In order to understand why some clades diversified during the Neogene while others dwindled in diversity, we must specify the order and timing of evolutionary branching events, as well as the ecological and geographical context of evolution and extinction in the contrasting groups. Such a phylogenetic understanding, in turn, hinges critically on a comprehensive account of the taxonomy of the groups in question.

The aim of this paper is to present a taxonomic review of all genera of Pseudolividae and to reassign genera that have been previously referred to the Pseudolividae or that were considered to belong to genera here assigned to that family. In the second part of the study (Vermeij & Carlson, in preparation), we present a phylogeny of

the group together with a narrative evolutionary and biogeographical history of the Pseudolividae.

PREVIOUS WORK

A comprehensive genus-level review of the Pseudolividae has not been attempted in more than fifty years. Cossmann (1901), Thiele (1929), and Wenz (1938–44) compiled the genera of the group, but they did not critically evaluate the limits of the taxa they recognized, and assigned most members of the Pseudolividae to the type genus *Pseudoliva*. Adegoke (1977) recognized the diversity of Paleocene and Eocene pseudolivids was too great to be accommodated in the genus *Pseudoliva* and its subgenus *Buccinorbis*, but he declined to propose new superspecific taxa. Although some of these groups were subsequently named (Zinsmeister, 1983; Squires, 1989; Squires et al., 1989), the naming of fossil members of the family proceeded piecemeal, and several superspecific taxa named earlier were overlooked. With the exception of Ponder and Darragh's (1975) paper on *Zemira*, which treated fossil as well as living species, most studies of Recent pseudolivids did not incorporate data on fossil forms.

Varying interpretations of the phylogenetic position of the Pseudolividae have contributed to confusion surrounding the taxonomic assignment of several genera, as well as to difficulties in defining the limits of the family. Perhaps because *Pseudoliva* has a smooth shell superficially resembling some members of the Olividae, many twentieth-century authors followed Swainson (1840) in placing *Pseudoliva* in or near the Olividae (see e.g. Melvill, 1903; Thiele, 1929; Wenz, 1938–44; Glibert, 1960; Taylor & Sohl, 1962; Sohl, 1964a, b; Ponder & Darragh, 1975; Adegoke, 1977; Ponder & Warén, 1988; Kilburn, 1989). Strongly sculptured genera such as *Luizia*, *Macron*, and *Triumphis* were therefore not recognized as pseudolivids, and were instead referred to the Buccinidae (Thiele, 1929; Douvillé, 1933; Wenz, 1938–44; Glibert, 1963; Addicott, 1970; Keen, 1971; Abbott, 1974).

In their treatment of gastropod genera, H. & A. Adams, (1853) assigned their new genus *Zemira* , together with *Pseudoliva* and its new subgenus *Macron*, to the muricid subfamily Purpurinae, a taxon encompassing genera that are assigned by modern authors to the muricid subfamilies Rapaninae and Ocenebrinae (see e.g. Kool, 1993; Vermeij & Kool, 1994; Vermeij, 1995; Vermeij & Vokes, 1997; Vermeij & Carlson, in preparation). This assignment was supported by characters of the radula and by the mistaken assertion that the opercula of these genera have a lateral nucleus, as do many muricids. Beyrich (1854) referred two small Lattorfian (= Priabonian, latest Eocene) species from North Germany to the genus *Purpura*, but he did not comment on his reasons for this assignment. One of these species, *P. pusilla*, was thought by Beyrich to lack the characteristic pseudolivid groove. Von Koenen (1889) referred the two species to *Pseudoliva*, pointed out that both exhibited the characteristic groove, and maintained that they have little in common with *Purpura*.

Sowerby (1846) was the first author to propose a close relationship between *Pseudoliva* and the Buccinidae. He considered *Pseudoliva* to be closely related to *Eburna* Lamarck, 1822 (non Lamarck, 1801), the buccinid genus known today as *Babylonia* Schlüter, 1838. Cossmann (1901) considered the Pseudolivinae as a subfamily of Buccinidae and included in it *Pseudoliva*, *Buccinorbis*, and *Fulmentum*; but he assigned *Zemira* and *Macron* to the Latruncilinae (= Babyloniinae) and *Triumphis* to the Cominellinae (= Photinae). Assignment of *Pseudoliva*, its subgenus *Buccinorbis*, and related Paleogene genera to the Buccinidae or Buccinoidea was accepted by von Koenen (1889), Fischer (1884), Böhm (1926), Palmer (1937), Gardner (1945), Golikov & Starobogatov (1975), Dockery (1977, 1880), and Squires (1989), among others. Shell characters formed the basis for most of these assignments.

Kantor's (1991) anatomical and phylogenetic study provided strong support for separating the Pseudolividae as a distinct family from other oliviform gastropods (see also Kantor, 1996). He isolated the group in a new suborder Pseudolivoidei, which together with the Muricoidei comprises the order Rachiglossa. Many derived features in Olividae, including pedal lobes, inner-whorl resorption, posterior mantle tentacle, mobile crescent-shaped propodium, and absence of the operculum, for example, are absent in Pseudolividae. Character states of Pseudolividae interpreted to be plesiomorphic for neogastropods include position of radular sac at base rather than near tip of proboscis, and (in *Benthobia*) the connection between the radular retractor muscle and the columellar muscle. In Pseudolividae, the proboscis is formed by elongation of the buccal tube, and there is a well defined Gland of Leiblein; whereas in the Muricoidei, which includes the Olividae and Buccinidae, the proboscis is formed by the elongation of the dorsal wall of the buccal cavity (Kantor, 1991).

The present study is based on shell characters. Many authors dismiss shell characters as unreliable for inferring phylogeny above the species level on the grounds that the shell is more subject to environmental variation and to evolutionary convergence than are the animal's internal organs. Not only is this argument predicated on untested and probably false assumptions, but it also effectively eliminates phylogenetic assessments of fossil forms. There can be no question that data on anatomy and on DNA sequences are immensely valuable in constructing classifications and phylogenies of living species; but they have only limited power in helping paleontologists make sense of the diversity of shells encountered in the fossil record. Instead of ignoring shell characters, we should evaluate the latter carefully. The aim of the present study is therefore to present a unified scheme of classification of both living and fossil pseudolivids based on a detailed analysis of shells.

MATERIALS AND METHODS

I have examined the type species of all but two genera of the Pseudolividae, as well as many additional species within and outside the family. A complete list of recognized species of Pseudolividae, together with material examined, is given in Appendix 1. Material of species discussed in this paper but not belonging to the Pseudolidae is listed in Appendix 2.

ABBREVIATIONS

ANSP	Academy of Natural Sciences, Philadelphia, Pennsylvania, USA
BMNH	The Natural History Museum, London, UK
CAS	California Academy of Science, San Francisco, California, USA
IGPS	Institute for Geology and Paleontology, Tohoku University, Sendai, Japan
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
LACM	Los Angeles County Museum of Natural History, Los Angeles, California, USA
MNHN	Muséum national d'Histoire naturelle, Paris, France
MGS	Mississippi Geological Survey, Jackson, Mississippi, USA
NM	Natal Museum, Durban, South Africa
PU	Purdue University, West Lafayette, Indiana, USA
PRI	Paleontological Research Institute, Ithaca, New York, USA
RGM	Nationaal Museum voor Natuurlijke Historie, Leiden, The Netherlands
SAM	South African Museum, Capetown, South Africa
SGO PI	Museo Nacional de Chile, Instituto de Palontologia, Santiago, Chile
TMM	Texas Memorial Museum, Austin, Texas, USA
UCMP	University of California Museum of Paleontology, Berkeley, California, USA
USNM	United States National Museum of Natural History, Washington, DC, USA
GJV	Vermeij collection
YPM	Yale Peabody Museum, New Haven, Connecticut, USA

SYSTEMATICS

Class Gastropoda
Subclass Prosobranchia
Order Neogastropoda
Superfamily Muricoidea Rafinesque, 1815
Family Pseudolividae Fischer, 1884

Diagnosis: Shell very small to large, maximum height 5 to 100 mm, ovate to fusiform; spire consisting of six or fewer teleoconch whorls; last whorl comprising 60% or more of total shell height; spiral sculpture usually present, consisting of a deep groove (pseudolivid groove) on basal half of last whorl, and of cords or threads that increase in degree of expression abapically; axial sculpture, when present, consisting of eight or more ribs per whorl, restricted to upper part of whorl; outer lip thin, sharp at edge, the adaxial layer not reflected over the edge to the abaxial side; pseudolivid groove terminating at edge of outer lip in blunt or sharp, ventrally directed tooth (labral tooth); outer lip often crenulated below labral tooth by terminations of grooves between basal cords; edge of outer lip planar, without sinuses except for adapical notch where outer lip joins penultimate whorl; inner lip smooth, adherent throughout its length to penultimate whorl, weakly concave, sometimes with weak fold at entrance of siphonal canal, sometimes with parietal tooth at adapical end; columellar and parietal callus variably expressed; living species with persistent periostracum.

Included genera: *Benthobia* Dall, 1889; *Buccinorbis* Conrad, 1865; *Fulmentum* Fischer, 1884; *Fusopsis* Ravn, 1939; *Fusulculus* Bouchet & Vermeij, 1997; *Luizia* Douvillé, 1933; *Hubachia* Etayo Serna, 1979; *Macron* H. & A. Adams, 1853; *Pseudoliva* Swainson, 1840; *Sulcobuccinum* d'Orbigny, 1850; *Sulcoliva* new genus; *Testallium* Vermeij & DeVries, 1997; *Triumphis* Gray 1857; *Zemira* H. & A. Adams, 1853.

Stratigraphic range: Late Cretaceous (Campanian) to Recent.

Discussion: *Characters:* None of the shell characters of the Pseudolividae is by itself unique to the family, but the constellation of characters serves to set the group apart from other neogastropod clades. Perhaps the most distinctive feature of the Pseudolividae is the so-called pseudolivid groove, a spiral depression on the lower part of the whorl that terminates in a ventrally and often adaxially projecting tooth (labral tooth) on the outer edge of the outer lip. The groove and tooth are obsolete in *Benthobia* and *Macron lividus*, and absent in *Triumphis*.

A labral tooth at the end of a groove is not unique to the Pseudolividae. It has also evolved numerous times in the Muricidae (many members of the subfamilies Muricinae, Ocenebrinae, and Rapaninae), Buccinidae (Pisaniinae of the genus *Cantharus* Röding, 1798, and related taxa; and Siphonaliinae of the Eocene genus *Phoracanthus* Cossmann & Martin *in* Martin, 1914), Echinofulgurinae (members of the genera *Cornulina* Conrad, 1853, and *Protobusycon* Wade, 1917), Fasciolariidae (the genus *Opcatostoma* Berry, 1958), Turbinellidae (the genus *Ceratoxancus* Kuroda, 1952), Olividae (many members of the subfamily Ancillinae), and various other buccinoids such as the Cretaceous genera *Buccinopsis* Conrad, 1857, and *Odontobasis* Meek, 1876, as well as the Recent *Tritonidea dentata* Schepman, 1911 (see e.g. Sohl, 1964a, b; Bouchet & Warén, 1985; Vignon, 1931; Vokes, 1990, 1992; Vermeij & Kool, 1994; Vermeij & Vokes, 1997; DeVries & Vermeij, 1997).

The simple, sharp-edged outer lip of fully grown

pseudolivids does not differ from that of ontogenetically younger individuals, and therefore indicates indeterminate growth according to the criteria set out by Vermeij and Signor (1992). The adult outer lip of *Triumphis* and of several large Eocene species of *Sulcobuccinum* is often adapically more extended than is that of individuals at earlier stages of growth, so that the spire comes to have a strongly concave lateral profile; but there is no evidence that growth in the spiral direction ceases at maturity, as would be the case in shells with determinate growth. Many pseudolivids (especially Eocene species of *Sulcobuccinum*) develop massive columellar and parietal callus deposits in adulthood, but again there is no evidence that growth at the outer lip ceases.

The indeterminate growth pattern of pseudolivids appears to be the plesiomorphic condition in neogastropods. It characterizes all Cretaceous buccinoids as well as Cenozoic Melongenidae, Turbinellidae, Fasciolariidae, Olividae (Ancillinae), and many clades within Muricidae, Buccinidae, and Conoidea, among others (see Vermeij & Signor, 1992).

The edge of the outer lip of Pseudolividae usually lies in a plane. Its contour is interrupted only by the emargination at the siphonal canal and by the adapical notch (see below). A planar outer lip also characterizes many Muricidae and Conidae. In many other neogastropods, the edge of the outer lip is medially convex downward, the convex sector being flanked adapically and sometimes abapically by a shallow, downwardly concave sinus. Variations on this more convex outer lip are found among Buccinidae, Mitridae, Costellariidae, Melongenidae, Nassariidae, Fasciolariidae, Turbinellidae, and many other groups.

In fully grown Pseudolividae, the smooth inner (adaxial) layer of the outer lip does not extend across the edge to the outer (abaxial) side. As a result, the edge is sharp and not glazed. This configuration occurs also in Muricidae, pisaniine Buccinidae, and Conidae, among others. The edge of the outer lip is polished smooth by the inner layer extending across it in most photine and babyloniine buccinids, nassariids, mitrids, and melongenids.

Nearly all members of the Pseudolividae are characterized by a posterior (or adapical) notch of the outer lip. This is an indentation where the outer lip joins the penultimate whorl at the adapical end of the aperture. A comparable notch occurs in many gastropods, including many muricine and rapanine muricids, columbellids, photine buccinids, melongenids, nassariids, mitrids, volutids, olivids, and conoideans. Within Pseudolividae, a few genera (*Benthobia*, *Fusulculus*, *Naudoliva*, and some large individuals of *Triumphis*) apparently lack a posterior notch.

Spiral sculpture in the Pseudolividae is usually better expressed on the lower part of the whorl than on the upper portion. As a result, crenulations at the ends of spiral grooves are most strongly expressed on the basal sector of the outer lip below the pseudolivid groove. This character state occurs widely among neogastropods including Columbellidae, many Buccinidae (Siphonaliinae, Photinae), Nassariidae, many Fasciolariidae, Costelariidae, Mitridae, Harpidae, and many Conoidea. In some Melongenidae, this pattern is superimposed on a spiral sculpture of keels or folds that decrease in prominence toward the base. In muricids and in the buccinid subfamily Pisaniinae, the strongest spiral sculptural elements always occur on the upper part of the whorl near the shoulder, decreasing both toward the base and from the shoulder to the suture above.

In Pseudolividae bearing axial sculpture, the axial elements are confined to the part of the last whorl above the pseudolivid groove. The restriction of axial sculpture to the upper part of the whorl is very widespread in Cretaceous neogastropods (Sohl, 1964a, b), and also characterizes many clades in the Buccinidae, Fasciolariidae, Nassariidae, Columbellidae, and Conoidea, among others.

The inner lip of Pseudolividae is smooth and always adherent above the siphonal fasciole, that is, its edge merges imperceptibly with the outer surface of the preceding whorl on which the inner lip encroaches during growth. Even when a thick callus is formed on the inner lip, as in species of *Sulcobuccinum* and *Pseudoliva*, the abaxial edge of the callus is rarely distinct. A smooth, adherent inner lip also characterizes Melongenidae, basal Conoidea, and many groups within Buccinidae, Muricidae, and Fasciolariidae (Fusininae). In most Olividae, including the Ancillinae, the inner lip is sculptured by thin, often very numerous spiral riblets; but a smooth inner lip occurs in the ancilline genus *Eburna* Lamarck, 1801.

In most Pseudolividae, the columella terminates abapically in a simple point on the left (adaxial) side of the siphonal canal or notch. This condition is widespread in Cretaceous buccinoids as well as in Cenozoic Buccinidae (Buccininae, Volutopsiinae) and basal Conoidea. In the pseudolivids *Macron* and *Triumphis*, however, there is a weak fold on the columella at the upper entrance of the siphonal canal. The abapical end of the columella therefore appears truncated in these genera. A basal columellar fold is very widespread in neogastropods including Muricidae, Fasciolariidae, and many Buccinidae (Pisaniinae and Siphonaliinae), but the truncation observed in *Macron* and *Triumphis* is less common, being best known in the Nassariidae and the buccinid subfamily Photinae (see Allmon, 1990).

The protoconch in most pseudolivids is paucispiral, here defined as having fewer than three whorls. The only genera with a multispiral protoconch are *Benthobia* and *Fusopsis*. Multispiral protoconchs are extremely widespread among Cretaceous buccinoids, and likely represent the primitive state of neogastropods in general and of the Pseudolividae in particular.

Comparisons with other Neogastropods: Some Pseudolividae superficially resemble the Olividae in having a posterior (adapical) notch, a relatively smooth shell, a low spire, and thick callus deposits on the columellar and

parietal regions. Members of the olivid subfamily Ancillinae further resemble pseudolivids in usually having a basal spiral groove (ancillid groove) and corresponding labral tooth. The ancillid groove is formed at the adapical margin of a broad, flat, somewhat raised zone (ancillid band) which is situated above the siphonal fasciole and which lacks the spiral cords or threads characteristic of pseudolivids. The labral tooth of Ancillinae lies at the entrance of the siphonal canal, whereas in Pseudolividae it is situated a short distance above the entrance of the canal, from which it is separated by a short crenulated sector of the outer lip. Olividae further differ from Pseudolividae in having most or all of the shell covered with a callus glaze, which is deposited by pedal lobes that are absent in Pseudolividae (Kantor, 1991).

Gardner (1945) thought that the Eocene genus *Ancillopsis* Conrad, 1865 (type species: *Ancillaria altilis* Conrad, 1832) might be closely related to *Pseudoliva*. This genus is characterized by an ovate, smooth, basally unconstricted shell, by a smooth concave columella, a posterior notch, and a distinct fasciolar band, above which a spiral groove ends in a slight tooth-like or lobe-like protrusion at the outer lip. *Ancillopsis* differs from Pseudolividae by having the spire covered with a glaze of callus, by the absence of a pseudolivid groove, and by lacking spiral and axial sculpture. Allmon (1990) showed that *Ancillopsis* does not belong with *Bullia* Gray *in* Griffith & Pidgeon, 1834, in the nassariid subfamily Dorsaninae, where Palmer (1937) and Palmer and Brann (1966) had placed it, because it lacks the terminal columellar fold characteristic of Nassariidae. *Ancillopsis* may be a divergent member of the Ancillinae.

The family Strepturidae Cossmann, 1901, has occasionally been subsumed under, or synonymized with, the Pseudolividae (see e. g. Ponder and Warén, 1988). Based on the type genus *Strepsidura* Swainson, 1840 (type species: *S. turgida* (Solander *in* Brander, 1766), the Strepturidae have in common with the Pseudolividae the following characters: spiral sculpture increasing in prominence toward the base, axial sculpture most prominent on upper part of whorl, and presence of small adapical notch. The Strepturidae differ, however, by the absence of a pseudolivid groove and labral tooth, and by having the inner shell layer reflected slightly over the outer lip's edge, which is therefore smooth and polished. Unlike most Pseudolividae, the Strepturidae have a very strong fold on the columella at the entrance of the siphonal canal. The genus *Melapium* H. & A. Adams, 1853, has often been included in either the Strepturidae (Cossmann, 1901) or Pseudolividae (Thiele, 1929; Wenz, 1938–44; Kilburn, 1989). As discussed later in this paper, I tentatively support Cossmann's (1901) assignment of *Melapium* to the Strepturidae. If this proves to be correct, then the anatomical study of *Melapium* by Kantor (1991) would imply that the Strepturidae, which are known mainly from the Paleogene, are relatively primitive neogastropods related to the Olividae.

Several members of the Melongenidae bear a close resemblance in shell characters to the Pseudolividae. Neogene to Recent genera such as *Melongena* Schumacher, 1817, and *Volema* Röding, 1798, share with pseudolivids a low-spired, indeterminately growing shell, a smooth columella without a basal fold, an adherent inner lip, a thick persistent periostracum, and a distinct adapical (posterior) notch in the outer lip. They differ from pseudolivids by lacking a basal groove and corresponding labral tooth as well as in the development of spiral sculpture. In melongenids, grooves ending in crenulations at the outer lip increase in prominence from the shoulder to the base, as in pseudolivids, but spiral keels or strong cords that often bear nodes or spines are most prominent on the upper part of the whorl.

In the Early Miocene (Aquitanian and Burdigalian) *Melongena lainei* (Basterot, 1825) from southwest France, the outer lip of the adult shell usually has a downwardly convex protrusion. In a few individuals, this protrusion, which corresponds to the basal constriction of the last whorl, bears a very weak, blunt labral tooth (for further discussion of this species see Peyrot, 1927; Vignon, 1931).

The genus *Cornulina* Conrad, 1853, contains several Late Paleocene and Eocene species with a "pseudolivid" groove and corresponding labral tooth. These include the type species, *C. minax* (Solander *in* Brander, 1766) from the Middle and Late Eocene of Europe and *C. armigera* (Conrad, 1833) from the Middle Eocene of the southeastern United States. Like members of the Pseudolividae, *Cornulina* is characterized by indeterminate growth, a sharp-edged outer lip, adherent smooth inner lip, and outer-lip crenulations that become more pronounced abapically. It differs from Pseudolividae by the absence of an adapical notch and by the presence of two prominent spiral rows of nodes, and from Eocene pseudolivids by the presence of a parietal rib and a basal columellar fold. Petuch (1994) interpreted *Cornulina* as an ancestor, or an early member of his subfamily Echinofulgurinae of the family Melongenidae. The earliest undoubted *Cornulina*, *C. praecursor* Cossmann, 1902, dates from the Thanetian stage of the Late Paleocene of the Paris Basin in France.

Protobusycon Wade, 1917, may be an even earlier genus in this group. The two Late Cretaceous members of this genus from the Gulf Coastal Plain of the United States (see Sohl, 1964a) bear a labral tooth at the end of a groove on the lower part of the last whorl. Suggestions that *Protobusycon* (type species: *Busycon cretaceum* Wade, 1917) belongs to the Turbinellidae (Bandel, 1993) or Ficoidea (Riedel, 1994) seem far-fetched. Turbinellids (especially Paleogene species) lack the parietal rib characteristic of *Protobusycon*. Ficoids, which Riedel (1994) argues are basal neogastropods, have internal shells without a labral tooth. The spines or nodes on the upper part of the whorl of *Protobusycon* indicate that the shell was probably external. Like *Cornulina*, *Protobusycon* differs from Paleogene pseudolivids by the presence of a parietal rib and the absence of a posterior notch. In contrast to the situation in Pseudolividae, axial sculpture in *Protobusycon* extends to the siphonal canal,

which is very long. Spiral sculpture generally decreases in strength adapically on the last whorl of *Protobusycon* as it does in pseudolivids, but two widely separated rows of nodes (one at the shoulder and one just above the tooth-bearing groove) are superimposed on this pattern, as they are in *Cornulina*. The single Paleocene species of *Protobusycon* (*P. judithae* Saul, 1988, from the "Martinez" stage of California) may not have possessed a labral tooth, but the genus could nonetheless have given rise to, or be the sister group of, *Cornulina*. In any case, the labral tooth of this group probably evolved independently from that in the Pseudolividae.

The genus *Lacinia* Conrad, 1853, comprises Middle Eocene shells remarkably similar in form to contemporaneous species of the pseudolivid genus *Sulcobuccinum* (see below). Like *Sulcobuccinum*, *Lacinia* has a low-spired, ovate, basally unconstricted, thick, indeterminately growing shell with a distinct adapical notch and extensive columellar and parietal callus. *Lacinia alveata* (Conrad, 1833) from the Gosport Sand (Middle Eocene) of Alabama, the type species of *Lacinia*, is a large species (maximum height 115 mm) characterized by a ventral protrusion on the outer lip about one-third the distance from the base of the shell. This protrusion corresponds to a very shallow, very broad spiral depression on the last whorl. Below this protrusion, the outer lip is finely crenulated. Unlike Paleogene pseudolivids, *Lacinia* has a distinct fold at the base of the columella. Moreover, this spiral sculpture is better expressed on the upper part of the whorl, where it consists of four broad, rounded folds. *Lacinia* is represented by two species in the Gosport Sand of Alabama, *L. alveata* and the much smaller *L. claibornensis* Palmer, 1937, a species with axial ribs on the spire whorls. Vredenburg (1922) has named three species of *Lacinia* from the Late Eocene and Oligocene of Burma and India. The Late Eocene Nigerian *Athleta lugardi* Newton, 1922, the type of *Laccinum* Eames, 1957, is very similar to *Lacinia* except that it lacks any trace of spiral sculpture.

Palmer (1937) and Wenz (1938–1944) assigned *Lacinia* to the Buccinidae, but the genus could equally well be included in the Melongenidae. It is even possible that *Lacinia* and *Laccinum* are divergent members of the Pseudolividae. For the time being, I consider their taxonomic placement uncertain.

There is also a considerable resemblance in shell characters between Pseudolividae and the buccinid subfamily Babyloniinae, as exemplified by the Eocene to Recent genus *Babylonia* Schlüter, 1838 (type species: *B. spirata* (Lamarck, 1822)). Like many Pseudolividae, *Babylonia* is characterized by a thick periostracum, canaliculate suture, relatively low spire, planar simple outer lip, a posterior notch, a well developed siphonal fasciole, smooth columella without basal fold, and a basally unconstricted last whorl. *Babylonia* differs from Pseudolividae by having the glossy inner (adaxial) layer of the outer lip reflected over the edge of the outer lip, so that the edge is smooth and polished rather than sharp; and by lacking basal spiral sculpture as well as a pseudolivid groove and labral tooth.

Members of the buccinid subfamily Pisaniinae have in common with pseudolivids a short spire, adherent periostracum, sharp-edged outer lip, smooth columella, and axial sculpture that is most strongly developed on the upper part of the whorl. Pisaniines differ from pseudolivids by having the spiral sculpture increasing in prominence from the base to the shoulder (adapically) rather than from the shoulder to the base (abapically), by having the edge of the outer lip ventrally convex instead of planar, and by lacking a posterior notch. Some Pisaniinae, such as the genera *Cantharus* Röding, 1798, and *Pollia* Gray *in* Sowerby, 1833, have a small labral tooth at the end of a spiral groove on the lower half of the last whorl, but this groove is a derived feature in the Pisaniinae and is therefore convergent with the labral tooth and groove of pseudolivids.

Shells of the buccinid subfamilies Photinae and Siphonaliinae differ from those of pseudolivids by having the edge of the outer lip polished rather than sharp in the fully grown shell, and usually by having a basal concave sector or sinus on the outer lip. Above this sinus, the outer lip of these buccinids is medially convex, and there is commonly a broad posterior sinus on the outer lip above the level of the shoulder. Some members of the Photinae, such as *Northia*, have a posterior notch at the upper end of this sinus. The siphonaliine genus *Phoracanthus* Cossmann & Martin *in* Martin, 1914 (type species: *Siphonalia ickei* Martin, 1914; Nanggulan beds, Eocene of Java) has a basal spiral groove ending in a labral tooth. Sculpture consists of fine spiral threads bundled into cords, and of widely spaced axial ribs on the upper part of the whorl (see Martin, 1914). It is likely that the labral tooth of *Phoracanthus* is convergent with that of Pseudolividae. A few species of Photinae also have a labral tooth. They include members of the genera *Cominella* Gray, 1850 (type species: *Cominella maculosa* (Martyn, 1784)) and *Iosepha* Tenison-Woods, 1879 (type species: *I. tasmanica* Tenison-Woods, 1879). In *Cominella acutinodosa* (Reeve, 1846) from Western Australia, a labral tooth is situated at the end of an enlarged central cord on the last whorl. In *Iosepha tasmanica* from southern Australia and *I. glandiformis* (Reeve, 1846) from New Zealand, a blunt labral tooth is formed at the center of the convex sector of the outer lip and does not correspond with either a cord or a groove. These labral protrusions are therefore not homologous with those of Pseudolividae.

Finally, the Muricidae differ from the Pseudolividae by having the spiral sculpture increasing in prominence from the base to the shoulder rather than from the shoulder to the base, and (in Paleogene forms) by lacking a posterior notch. In early muricids, moreover, axial sculpture almost always extends from the suture to the base, and is not confined to the upper part of the whorl. No muricids have the thick, persistent periostracum typical of pseudolivids.

KEY TO GENERA OF PSEUDOLIVIDAE

1a Protoconch multispiral (three whorls or more) 2
1b Protoconch paucispiral (less than three whorls) 3
2a Shell fusiform, relatively slender (height-to-diameter ratio 2.0); spiral sculpture consisting of fine cords ..... *Fusopsis*
2b Shell inflated (height-to-diameter ratio 1.4 to 1.6); spiral sculpture obsolete ..... *Benthobia*
3a Inner (adaxial) side of outer lip lirate (bearing spiral riblets) 4
3b Inner side of outer lip smooth or unknown ... 6
4a Shell moderately slender (height-to-diameter ratio 1.7 to 1.9); axial sculpture present on upper part of whorls; parietal rib absent; abapical end of columella pointed ..... *Luizia*
4b Shell relatively broad (height-to-diameter ratio 1.4 to 1.8); axial sculpture absent or confined to early whorls; parietal rib present; abapical end of columella with distinct fold 5
5a Pseudolivid groove and labral tooth absent; axial sculpture present on early whorls; outer lip adapically extended at maturity ..... *Triumphis*
5b Pseudolivid groove and labral tooth present (but obsolete in *Macron lividus*); axial sculpture absent; outer lip not adapically extended at maturity ..... *Macron*
6a Pseudolivid groove situated low on last whorl; parietal rib present 7
6b Pseudolivid groove situated high on last whorl; parietal rib absent 9
7a Spiral sculpture present on whole surface of last whorl; axial sculpture present on early whorls, or expressed as strong growth lines on last whorl; columellar callus thin, of limited extent ..... *Testallium*
7b Spiral sculpture on last whorl absent; axial sculpture absent; columellar callus thick, extensive 8
8a Parietal rib rounded, not markedly constricting adapical end of aperture ..... *Pseudoliva*
8b Parietal rib lamella-like, sharp-edged, separating long adapical channel from rest of aperture ... . *Fulmentum*
9a Siphonal fasciole absent; siphonal notch very shallow 10
9b Siphonal fasciole present; siphonal notch deep .. 11
10a Suture linear, appressed; base of last whorl constricted; labral tooth obsolete; axial sculpture present on upper part of whorl ..... *Fusuleulus*
10b Suture deeply channeled; base of last whorl not constricted; labral tooth prominent; axial sculpture usually absent ..... *Zemira*
11a Shell high-spired (last whorl comprising 60 to 70% of total shell height); pseudolivid groove indistinct; labral tooth present; last whorl constricted at base; columellar callus thin 12
11b Shell high-spired to low-spired; last whorl usually not constricted at base; pseudolivid groove and labral tooth distinct; columellar callus well developed, thick 13
12a Adapical notch absent; axial sculpture absent or consisting of short ribs at shoulder ... *Naudoliva*
12b Adapical notch weak but present; axial sculpture consisting of narrow peripheral band of beads on last whorl ..... *Sulcoliva*
13a Deep groove situated immediately below sharply angled shoulder; aperture very wide .... *Hubachia*
13b Shoulder variably developed, without deep groove immediately below it; aperture narrower ..... *Sulcobuccinum*

Genus *Pseudoliva* Swainson, 1840
(Figures 10–12)

Type species: *Buccinum plumbeum* Chemnitz (= *Buccinum crassum* Gmelin, 1791) by monotypy.

Synonyms:
Gastridium Sowerby, 1842 (type species: *B. plumbeum* Chemnitz), *non* Modeer, 1793, *nec* Sowerby, 1846.

Diagnosis: Shell moderately large, maximum height 50 mm, ovate to globose; protoconch paucispiral; spire moderately low to very low, last whorl comprising 78 to 90% of total shell height; last whorl rounded above, not constricted basally; spiral sculpture confined to early teleoconch whorls, absent on last whorl; axial sculpture absent; pseudolivid groove situated low on last whorl; outer lip with distinct labral tooth, without basal crenulations; inner side of outer lip smooth; posterior notch deep; aperture ovate, its height-to-breadth ratio 2.1; columellar and parietal callus moderately thick, well developed ventrally, but not extending onto spire; parietal rib strong, rounded; siphonal fasciole low, rounded; anterior notch deep; umbilicus absent.

Stratigraphic and geographic distribution: Early? Miocene, Madeira; Early Pliocene to Recent, southern Africa.

Discussion: Although Swainson (1840: 82, 306) proposed the name *Pseudoliva* for the West African species we know today as *Pseudoliva crassa* (Gmelin, 1791), *Pseudoliva* was interpreted broadly by paleontologists, who included in it a diverse array of gastropods with a basal groove and corresponding labral tooth. I follow Kilburn (1989) in restricting *Pseudoliva* to a small group of warm-temperate to subtropical West African species characterized by a non-umbilicate, smooth or obsoletely spirally threaded, ovate shell with a posterior notch, parietal rib, well developed callus, and smooth inner (adaxial) side of the outer lip. *Pseudoliva* differs from *Sulcobuccinum* by having the pseudolivid groove and labral tooth situated lower on the whorl, by the presence of a rounded parietal rib at the adapical end of the inner lip, and by being essentially smooth, there being no trace of

axial sculpture. *Sulcobuccinum kitsoni* (Newton, 1922) from the Ameki Formation (Middle Eocene) of Nigeria shows a trace of the parietal rib, and may be transitional between *Sulcobuccinum* and *Pseudoliva*. In the related genus *Fulmentum*, the parietal rib has become exaggerated as a plate, which sets a long, channel-like adapical section off from the rest of the aperture. *Pseudoliva* differs from *Testallium* by lacking spiral sculpture on the last whorl and by not having the last whorl constricted at the base.

I recognize three species in the genus *Pseudoliva* (see Appendix). The type species, *P. crassa*, is known only from the coast of Angola. The largest specimen I have seen (height 49.0 mm) comes from the Baia dos Tigres. Kensley and Pether (1986) described a very closely related if not identical form as *Pseudoliva lutulenta* from the 50 m level (Early Pliocene; J. Pether, personal communication) at Hondeklip, on the west coast of South Africa. The earliest member of the genus appears to be *P. orbignyana* Mayer, 1864, from deposits of probably Early or Middle Miocene age on Madeira.

Kilburn (1989) synonymized *Sylvanocochlis* Melvill, 1903, with *Pseudoliva*. Its type species, *Pseudoliva ancilla* Hanley, 1859, from the Agulhas Bank off South Africa, differs from *Pseudoliva* by its high spire and adapically extended aperture. As discussed below under *Fulmentum*, I consider *Sylvanocochlis* a synonym of *Fulmentum*.

Genus *Fulmentum* Fischer, 1884

Type species: *Buccinum sepimentum* Rang, 1832.

Synonym:

Sylvanocochlis Melvill, 1903 (type species: *Pseudoliva ancilla* Hanley, 1859).

Diagnosis: Shell of moderate size, maximum height 40 mm, ovate; spire moderately low, last whorl comprising 75 to 88% of total shell height; last whorl evenly rounded above, weakly or not constricted basally; spiral sculpture usually absent, sometimes expressed as very weak threads below pseudolivid groove; axial sculpture absent; pseudolivid groove situated low on last whorl; outer lip with distinct labral tooth, below which small crenulations may appear; inner side of outer lip smooth; posterior notch present; aperture ovate (*F. sepimentum*) to elongate-ovate (*F. ancilla*), its height-to-breadth ratio 2.4 to 3.0; adapical end of aperture extended as narrow channel between outer lip and a prominent, projecting, plate-like parietal ridge at posterior end of inner lip; columellar and parietal callus well developed ventrally, but not extending onto spire; siphonal fasciole low, rounded, sculptured by five weak spiral threads; anterior siphonal notch deep; umbilicus absent.

Stratigraphic and geographic distribution: Recent, tropical West Africa and temperate South Africa.

Discussion: Fischer (1884: 632) introduced *Fulmentum* as a subgenus of *Macron* for *Buccinum sepimentum* Rang, 1832, a Recent species from tropical West Africa. Most later authors have treated *Fulmentum* as a full genus or as a subgenus of *Pseudoliva*. The exaggerated, plate-like parietal ridge, which sets apart a narrow adapical extension from the rest of the aperture, readily distinguishes *Fulmentum* from *Pseudoliva*. *Fulmentum sepimentum* ranges from Cotonou (Togo) to southern Angola. The largest specimen I have seen (height 20.4 mm) is from Pointe Noire, Congo (MNHN).

Melvill (1903: 325) named the genus *Sylvanocochlis* for *Pseudoliva ancilla* Hanley, 1859, a relatively large (maximum height 40 mm), high-spired species from the Agulhas Bank off South Africa. Kilburn (1989) considered *Sylvanocochlis* a synonym of *Pseudoliva*, correctly pointing out that spire height in *Pseudoliva* is quite variable and therefore an unreliable criterion for the recognition of genera. My examination of *Pseudoliva ancilla* prompts me to assign this species to *Fulmentum*. Like *F. sepimentum*, the South African species has a drawn-out adapical extension of the aperture, set off from the abapical main portion of the aperture by a flange-like parietal lamella. *Fulmentum ancilla* differs from *F. sepimentum* by being about twice as large and by not being constricted basally.

Genus *Sulcobuccinum* d'Orbigny, 1850

Type species: *Buccinum fissuratum* Deshayes, 1835, here designated (Figures 1–3).

Synonyms:

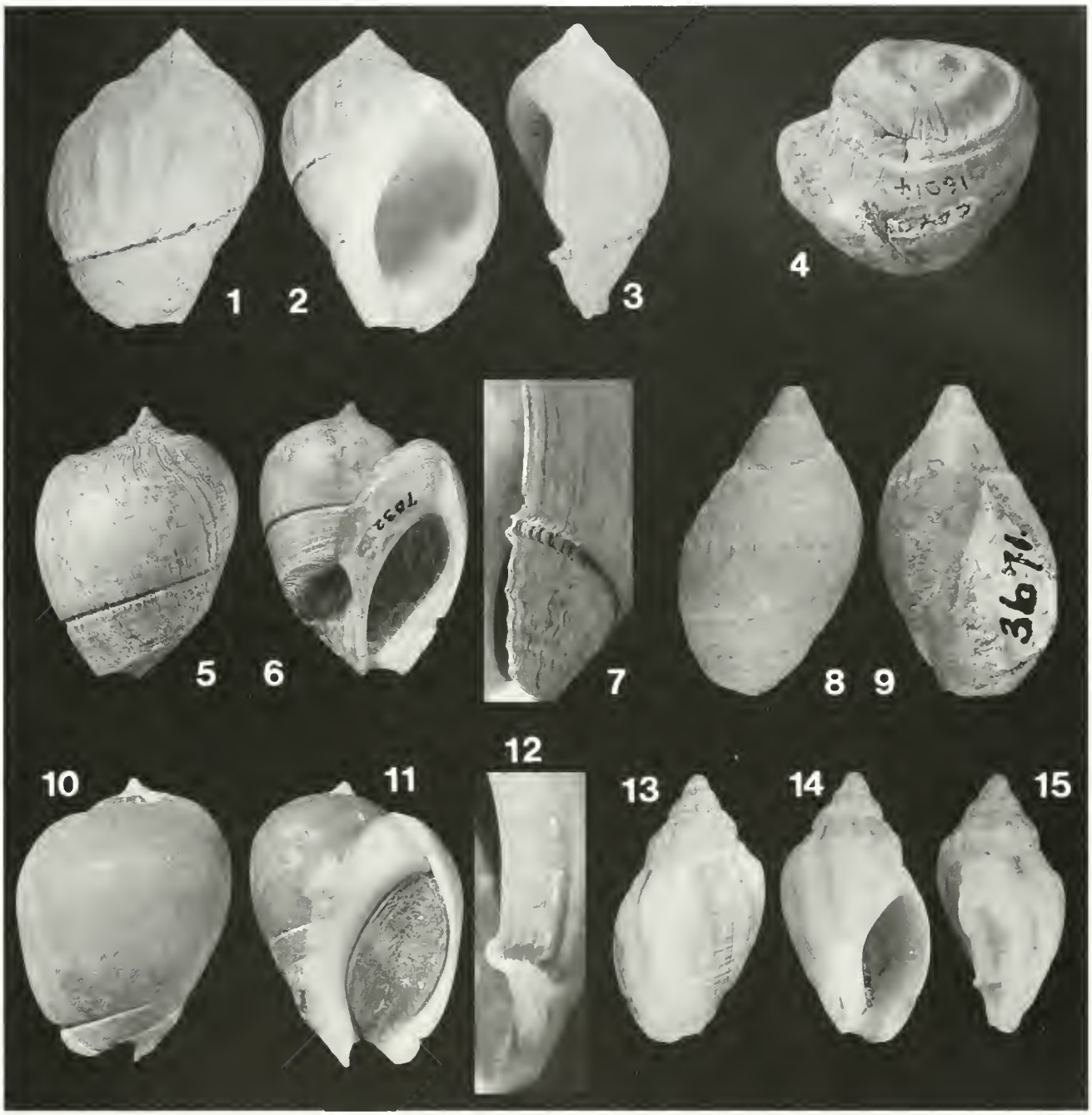
Buccinorbis Conrad, 1865 (type species: *Buccinum vetustum* Conrad, 1833, subsequent designation by Cossmann, 1901; Figures 5–7).

Pegocomptus Zinsmeister, 1983 (type species: *Molopophorus howardi* Dickerson, 1914, by original designation).

Calorebama Squires, 1989 (type species: *Pseudoliva dilleri* Dickerson, 1914, by original designation).

Popenoeum Squires, Zinsmeister & Paredes-Mejia, 1989 (type species: *Popenoeum maritimus* Squires, Zinsmeister & Paredes-Mejia, 1989, by original designation).

Diagnosis: Shell very small to large, maximum height 4.2 to 66 mm, ovate to globose; protoconch paucispiral; spire relatively high to low, last whorl comprising 63 to 100% of total shell height; last whorl rounded or shouldered above, usually not constricted at base; spiral sculpture variably expressed; axial sculpture consisting of eight or more ribs per whorl, confined to part of whorl above pseudolivid groove, and often forming nodes or spines at shoulder and at intersections with spiral cords; axial sculpture confined to spire whorls in some species; pseudolivid groove at relatively high position, not less than one-fourth from abapical end of last whorl; outer lip with distinct labral tooth, below which are three to five crenulations corresponding to grooves between basal cords; inner side of outer lip smooth; posterior notch present; aperture ovate to ovate-elongate, its height-to-breadth ratio 2.0 to 3.8; columellar and parietal callus variably expressed, often thick and extending onto spire in large Eocene species; parietal ridge absent; siphonal



Figures 1–3. *Sulcobuccinum fissuratum* (Deshayes, 1835); Châlons-sur-Vesle, Marne, France; Thanetian; MNHN. Shell height 38 mm.

Figure 4. *Hubachia ramirolobae* Etayo Serna, 1979, Paleocene, Colombia; UCMP 16014. Oblique view of apex; total shell height 30 mm.

Figures 5–7. *Buccinorbis vetusta* (Conrad, 1865); Little Stave Creek, Alabama; Gosport Sand (Middle Eocene); GJV. Shell height 36 mm.

Figures 8–9. *Sulcoliva monilis* (Olsson, 1928); Parinas Sandstone (Early Eocene, Peru); PRI 3671. Shell height 17 mm.

Figures 10–12. *Pseudoliva crassa* (Gmelin, 1791); West Africa; CAS 063184. Shell height 25 mm.

Figures 13–15. *Luizia zebrina* (A. Adams, 1855); Ilha de Luana, Angola; MNHN. Shell height 14.2 mm.

fasciolar ridge present or obsolete, bounded above by keel when present; anterior siphonal notch usually deep; umbilicus present or absent.

Stratigraphic and geographic distribution: Late Cretaceous (Campanian and Maastrichtian) of Europe, North Africa, southwestern Asia, and western South America; Early Paleocene to Late Eocene (Danian to Priabonian) of Europe, western and eastern North America, South America, North and sub-Saharan Africa; Early Paleocene of India; Late Eocene to Early Oligocene of Japan; ?Early Oligocene of Peru.

Discussion: The taxonomy, relationships, and generic nomenclature of Late Cretaceous and Paleogene pseudolivids remain matters of controversy and uncertainty. All species of this age are characterized by a pseudolivid groove that is situated at a relatively high position on the whorl, and by the absence of a parietal rib. In these important respects, they differ from the type genus *Pseudoliva*. In addition, Cretaceous and Paleogene pseudolivids usually show traces of axial sculpture, although it may be confined to apical whorls, especially in Eocene species. There is great variation in the degree of development of spiral and axial sculpture, in the presence or absence of a siphonal fasciole, in the height of the spire, and in the development of a subsutural channel. Many species have nodes or even spines at the shoulder or at the adapical ends of axial ribs, but in some species the upper part of the whorl is rounded and therefore unshouldered, and nodes are not developed.

Several authors have attempted to subdivide this group into genera, subgenera, or species groups. Among Paleocene and Eocene species with axial sculpture on the last whorl, Adegoke (1977) recognized but did not name a group of Paleocene species based on *Pseudoliva rogersi* Adegoke, 1977, from the Ewekoro Formation of Nigeria. It is characterized by reticulate sculpture, in which several rows of nodes form where strong spiral cords intersect axial riblets. Zinsmeister (1983) proposed the genus *Pegocomptus* for a very similar species, *Molopophorus howardi* Dickerson, 1914, from the Santa Susana Formation of southern California and the Sepultura Formation of Baja California Norte, Mexico. My examination of this Paleocene species shows that it lacks an umbilicus, whereas *Pseudoliva rogersi* has a wide, deep umbilicus (Adegoke, 1977).

Squires (1989) distinguished a second group of axially ribbed Paleocene and Eocene pseudolivids as his new genus *Calorebama*, for which he chose *Pseudoliva dilleri* Dickerson, 1914, as type. He characterized *Calorebama* as having an angulated, noded shoulder, shallow appressed suture, pseudolivid groove situated relatively high on the last whorl, and variably developed spiral sculpture that coarsens toward the base. Squires included in this group two species (*C. unicarinata* and *C. tuberculifera*) from the Paleocene of the Gulf Coastal Plain of the United States, as well as five subspecies of *C. dilleri* from the Eocene of western North America. Kase (1990) added his new species *C. cretacea* from the Late Cretaceous (Campanian to Early Maastrichtian) of Japan. He included this species in *Calorebama* because of its resemblance to *C. dilleri inornata*, which like *C. cretacea* lacks shoulder nodes.

At least two of the characters of *Calorebama* mentioned by Squires (1989) are not generically diagnostic. All pseudolivids have spiral sculpture that coarsens toward the base, and a nodose shoulder, which occurs in many Late Cretaceous and later pseudolivids, is often variably expressed during ontogeny (Squires, 1989). A third character, the appressed suture, occurs in *Pegocomptus* as well as in several slender species of the *Pseudoliva koeneni* group (see below), in which the shoulder is not nodose.

Still another group that was recognized in this early welter of pseudolivids was *Popenoeum* (Squires et al., 1989). This genus, typified by *P. maritimus*, was characterized as having tabulate whorls, subsutural channel, axial ribs terminating as tubercles at the shoulder, a relatively thick columellar callus, and a well developed siphonal fasciole. Besides the type species and its subspecies *P. m. bajaensis*, Squires et al. (1989) included a wide variety of Cretaceous to Eocene species: *P. bocaserpentis*, *P. chavani* (Glibert, 1973, not Tessier, 1952; see below), *P. mutabilis* and its subspecies *woodsi*, *P. prima*, *P. robustum*, *P. scalina*, and *P. subcostata* (see Appendix 1). Kase (1990) subsequently assigned the Cretaceous species *P. praecursor* and *P. zitteli* to *Popenoeum*. Squires et al. (1989) explicitly excluded *P. mutabilis douvillei* from *Popenoeum*, apparently because of the extraordinary development of callus on the spire of that large Early Eocene form from Peru. My examination of the holotypes of *Pseudoliva mutabilis douvillei* and *P. m. woodsi* reveals broad similarities in shell shape and in the development of axial sculpture, and supports Olsson's (1928) suggestion that these two forms are closely related to each other and to *P. m. mutabilis*. *Pseudoliva mutabilis douvillei* has more prominent spines, which are directed abaxially, than does *P. m. woodsi*, whose spines are adapically directed.

Glibert (1973) defined an informal group of axially ribbed Paleocene pseudolivids as the group of *Pseudoliva koeneni*. Members of this European group are characterized by very small, slender shells with a linear rather than canaliculate suture. Most species, including *P. koeneni*, *P. elisae*, and *P. tenuicostata*, lack shoulder tubercles, but *P. curvicostata* does possess tubercles (see Glibert, 1973). Some of these species may be synonyms of each other, and some may prove to belong to *Fusopsis*, which is distinguished from other axially ribbed Paleogene pseudolivids by having a multispiral rather than paucispiral protoconch.

Many Late Cretaceous and Paleocene pseudolivids with axial sculpture on the last whorl were left out of these formal and informal groups. Some species combine features of several nominal groups. *Buccinum fissuratum* Deshayes, 1835, from the Late Paleocene (Thanetian) of the Paris Basin, for example, has a canaliculate suture like that of *Popenoeum*, but unlike *Popenoeum* it

has a rounded shoulder lacking nodes or tubercles. Spiral sculpture appears to be confined to the area below the pseudolivid groove, and is expressed at the edge of the outer lip as three crenulations. A siphonal fasciole is absent, as in *Calorebama dilleri kirbyi* and *Purpura pusilla*. *Buccinum laudunensis* Defrance, 1826, also from the Thanetian of the Paris Basin, is very similar *to B. fissuratum*, but its suture is appressed rather than canaliculate, and there is a low, distinct siphonal fasciole.

Moreover, the nominal groups differ in characters that vary intraspecifically and even during individual ontogeny. Wrigley (1941), for example, argued convincingly that a single Late Eocene species from northwestern Europe (Germany, Belgium, and England) is represented by a continuous series of forms between the types that have been called *Purpura nodulosa*, in which eight to ten axial ribs per whorl are enlarged by two rows of nodes, and *P. pusilla*, in which the axial riblets are smooth (see Beyrich, 1854). This species also varies in the expression of spiral sculpture below the pseudolivid groove (Wrigley, 1941). In many species, spiral sculpture covers most or all of the surface of the last whorl in ontogenetically young individuals, but it becomes restricted to the base in ontogenetically older ones. When describing *Pseudoliva libyca*, Quaas (1902) noted that young, strongly sculptured slender, high-spired individuals have a quite different appearance from larger individuals of the same species, in which the lateral profile of the relatively low spire is concave. Squires (1989) observed ontogenetic changes in spiral sculpture and in the presence of a subsutural swelling in species that he assigned to *Calorebama*.

It is therefore difficult to delineate well defined groups based on such characteristics as spire height, expression of spiral and axial sculpture, and presence of nodes among Cretaceous and Paleogene pseudolivids with axial sculpture. Although several lineages may be represented in this group, I prefer to treat the early, axially ribbed pseudolivids with a paucispiral protoconch as members of a single genus-level group.

In some Paleocene and Eocene pseudolivids, axial sculpture is confined to the spire whorls or is occasionally absent. Palmer (1937) used the taxon *Buccinorbis* Conrad, 1865, to encompass this group. Like Cossmann (1901) and Adegoke (1977), she regarded *Buccinorbis* as a subgenus or section of *Pseudoliva*. Fischer (1884) and Thiele (1929) synonymized *Buccinorbis* with *Pseudoliva*, whereas Squires (1989) and Vermeij and DeVries (1997) considered it to be a distinct genus. Conrad (1865:21) introduced *Buccinorbis* as a subgenus of *Sulcobuccinum* without diagnosis or comment. He included in it all eastern North American pseudolivids described up to 1865, including strongly sculptured species like *Pseudoliva tuberculifera* as well as the nearly smooth *Buccinum vetustum*. Cossmann (1901) designated *B. vetustum* Conrad, 1833, the last species Conrad (1865) listed as belonging to *Buccinorbis*, as type species.

The only character distinguishing *Buccinorbis* from most other early pseudolivids is the absence of axial sculpture on the last two teleoconch whorls. Species vary in the presence or absence of spiral sculpture on the upper part of the whorl, in spire height, in the presence or absence of an umbilicus, and in the development of columellar and parietal callus deposits. As pointed out by Olsson (1928), Palmer (1937), and Gardner (1945), these attributes vary during ontogeny, just as the expression of axial sculpture does. Ontogenetically young shells tend to be high-spired, to be axially sculptured, to have spiral cords or threads distributed over the whole surface of the whorl, to have an open umbilicus, and to have a relatively limited callus. The loss of axial sculpture likely occurred in several Paleocene lineages, and by itself does not constitute sufficient grounds for distinguishing *Buccinorbis* from other early pseudolivids with a paucispiral protoconch, high position of the pseudolivid groove on the whorl, and absence of a parietal rib. I therefore treat most of these species as belonging to a single genus.

The oldest available generic name for this group of pseudolivids is *Sulcobuccinum* d'Orbigny, 1850. This name has been overlooked by most authors, perhaps in part because Fischer (1884), Cossmann (1901), Thiele (1929), and Wenz (1938–44) synonymized it with *Pseudoliva* without discussion. D'Orbigny (1850:303) compared his genus with *Buccinanops* d'Orbigny, 1841 (Nassariidae, Dorsaninae; see Allmon, 1990), and listed three species as belonging to it: *Buccinum fissuratum* Deshayes, *B. tiara* Deshayes, and *B. semicostatum* Deshayes. Among these, *B. semicostatum* is a junior synonym of *Buccinum laudunense* Defrance (see Glibert, 1960; Villatte, 1970), and *B. tiara* is a junior synonym of *Struthiolaria prima* Defrance (Villatte, 1970). Coquand (1862) added a fourth species, *S. michelini*; and Conrad (1865) introduced *Buccinorbis* as a subgenus of *Sulcobuccinum*. Neither d'Orbigny (1850) nor any subsequent author designated a type species of *Sulcobuccinum*. Because *Buccinum fissuratum* Deshayes, 1835, was the first species listed by d'Orbigny (1850), I here designate it as the type species of *Sulcobuccinum* d'Orbigny, 1850.

Several genera have in common with *Sulcobuccinum* the presence of axial sculpture on the last whorl. These include *Benthobia*, *Fusopsis*, *Fusulculus*, *Hubachia*, *Luizia*, and *Sulcoliva*. As discussed further under *Fusopsis*, *Sulcobuccinum* differs from that Paleocene group mainly by having a paucispiral protoconch rather than a multispiral one. Most species of *Sulcobuccinum* are not basally constricted, in contrast with *Fusopsis*. The study of protoconchs may reveal a diversity of types among species currently assigned to *Sulcobuccinum*. In addition, further work may show that *Fusopsis* is conchologically indistinguishable from *Benthobia*. *Sulcobuccinum* differs from *Fusulculus* by the presence of a posterior notch on the outer lip and by lacking the basal constriction of the last whorl. It differs from *Luizia* by the absence of riblets on the inner side of the outer lip, and from *Sulcoliva* by having a deep psendolivid groove and by not having axial ribs confined to a narrow peripheral band.

In reviewing the species here assigned to *Sulcobuc-*

cinum, I have uncovered a case of homonymy. Glibert (1973) named *Pseudoliva chavani* from the Calcaire de Mons (Danian, Early Paleocene) of Belgium. Unfortunately, this name is preoccupied by *Pseudoliva* (*Buccinorbis*) *chavani* Tessier, 1952, from the Maringot de Balling (Paleocene) of Senegal. I therefore rename Glibert's species *Sulcobuccinum multinodulosum*, new name, to emphasize the large number (seventeen to nineteen) of axial riblets forming nodules below the suture.

Nearly all Late Cretaceous species of *Sulcobuccinum* are known from the Old World (see Appendix 1). These include *S. aaronsohni* and *S. moabiticum* from the Senonian of Palestine, *S. cretaceum* from the Campanian to Early Maastrichtian of Japan, *S. praecursor* and *S. zitteli* from the Senonian of Hungary, *S. sofeggincnse*, *S. libycum*, and *S. subcostatum paucicostatum* from the Maastrichtian of North Africa, and *S. ambiguum* from the type Maastrichtian in the Netherlands and perhaps the Maastrichtian of Tunisia (for species accounts see Quaas, 1902; Pervinquière, 1912; Blanckenhorn, 1927; Rossi Ronchetti, 1959; Kase, 1990). Although I have not examined these Late Cretaceous species, the differences among them seem slight, and there may be many fewer species than there are available names. The only New World members of *Sulcobuccinum* from the Late Cretaceous are Olsson's (1934) *Pseudoliva* sp. from the Maastrichtian of northern Peru, represented by a single, poorly preserved specimen, and Muniz's (1993) *Pseudoliva bellecompta*, a cancellate species from the Gramame Formation (Campanian) of northeastern Brazil. Oddly enough, the genus is unknown from the Cretaceous of sub-Saharan Africa, Madagascar, and North America. All Cretaceous species have a relatively high spire, the last whorl comprising 80% or less of the total shell height, and all have well developed axial sculpture on the spire whorls as well as the last whorl.

During the Paleocene, the genus *Sulcobuccinum* was widely distributed in warm seas, with an apparent center of diversity around the North Atlantic (see Appendix 1). Species such as *S. koeneni* from Denmark, *S. multinodulosum* from Belgium, *S. rosenkrantzi* from Austria, and *S. minutissimum* from Morocco are high-spired, axially ribbed, very small forms not exceeding 7 mm in shell height. By contrast, the European *S. prima* reaches a height of 65 mm and has a spinose shoulder.

Several Old World Paleocene species show trends toward a reduction in axial sculpture. One such group of species is represented in the Ewekoro Formation of Nigeria by *S. adelekei*, *S. f. funkeanum*, and *S. f. ornatum*. Adegoke (1977) characterized this group as high-spired, spirally sculptured, and having a narrow elevated callus and a rounded rather than shouldered upper part of the whorl. These Paleocene species are small (maximum height of *S. adelekei*, USNM 174853, 12.0 mm). In the Ameki Formation (Middle Eocene) of Nigeria, this group is represented by the larger *S. kitsoni* (maximum height 47.4 mm). This is a high-spired species (last whorl comprising 70 to 80% of total shell height) with a parietal swelling at the adapical end of the inner lip. Related Eocene species include *S. thielei* and *S. leutweini* from Namibia and *S. eschi* from Cameroon. Böhm (1926) described *S. thielei* as having an umbilicus, a moderately high spire (last whorl comprising 84% of total shell height), relatively large size (maximum height 50 mm), and spiral sculpture persisting on the last whorl only near the suture and below the pseudolivid groove. Besides being slightly lower-spired, *S. thielei* appears to be very similar to *S. kitsoni* and probably represents the same species, which would then take the name *S. kitsoni* (Newton, 1922).

A second group in which axial sculpture has become reduced is represented in the Ewekoro Formation of Nigeria by *S. guineense*. This species has a minute, very low spire, a well developed callus extending on the spire, a distinct siphonal fasciole, and axial sculpture consisting of fifteen to sixteen ribs on spire whorls but absent on the last two whorls. The slightly older *S. chavani* from the Danian (Early Paleocene) of Senegal is very similar, but its axial sculpture extends to the last whorl (see Tessier, 1952). *Sulcobuccinum guineense* and the *S. adelekei* group represent two apparently independent transitions from typical *Sulcobuccinum* in which axial sculpture continues to adulthood, to the *Buccinorbis* phenotype, in which the last one or two whorls are free of axial sculpture.

Eocene representatives of *Sulcobuccinum* were highly diverse in form and size. Strongly tuberculate or spiny species include *S. mutabile* and its subspecies *S. m. woodsi* and *S. m. douvillei* from the Early and Middle Eocene of Peru (see Olsson, 1928; Squires *et al.*, 1989) and *S. michelini* from the Middle Eocene (Suessonian) of North Africa (for discussion see Salvan, 1954). Small, slender, axially ribbed species include *S. bussoni* from the Early Eocene of southern Tunisia (see Albanesi & Busson, 1974) and *S. pusillum* from the Lattorfian (latest Eocene) of northwestern Europe. The name *Purpura pusilla* Beyrich, 1854 (pp. 143–144) has page priority over the synonymous *P. nodulosa* Beyrich, 1854 (p. 144), and must therefore stand as the valid name for this small, sculpturally variable species. Relatively low-spired species with a tuberculate shoulder and variably developed axial sculpture on the last whorl include *S. schweinfurthi* from Cameroon (see Oppenheim, 1904) and the forms that Squires (1989) subsumed under the name *Calorebama dilleri* from the Early to Late Eocene (Ypresian to Priabonian) of western North America. These western North American forms overlap greatly in form, sculpture, and stratigraphic distribution (Squires, 1989), and may well represent a single, variable, stratigraphically long-lasting, widely distributed species whose earliest valid name is *Sulcobuccinum lineatum* (Gabb, 1864). A large (perhaps 50 mm high), axially ribbed species without a tuberculate shoulder from the latest Eocene (Lattorfian) of Helmstedt, Germany, was described as *Pseudoliva rudis* on the basis of one poor specimen by von Koenen (1889). The distinctive Middle Eocene *S. coronaria* from Peru is characterized by large size

(height 50 mm), a high spire, and a nodose, sharply shouldered last whorl (see Olsson, 1930). Several species groups of *Sulcobuccinum* lack axial sculpture on the last one or more teleoconch whorls, and were therefore previously assigned to the genus, subgenus, or section *Buccinorbis*. Besides *S. kitsoni*, which I discussed above, this group includes many species in North and South America, Europe, and one in Japan.

The Old World group of slender species of the *Buccinorbis* phenotype, typified by *S. adelekei* and *S. kitsoni* (see above), is represented in the early Eocene of the Gulf Coastal Plain of the United States by *S. ostrarupis* from Alabama and by the Texan subspecies *S. o. pauper*. These forms have a high spire (last whorl comprising 67% to 76% of total shell height), a narrow aperture, and an obsolete pseudolivid groove. The last whorl is rounded above and evenly tapered below, and lacks an umbilicus and siphonal fasciole. It is possible that some of these characters are those of juvenile specimens, but another possibility is that the *S. ostrarupis* group is plesiomorphic with respect to features of the spire and base.

The species group of *S. vetustum* (type species of *Buccinorbis*) occurs on the Gulf Coastal Plain of the southeastern United States (see Palmer, 1937; Dockery, 1980). *Sulcobuccinum vetustum*, from the Gosport Sand (Middle Eocene) of Alabama, has an appressed suture, closed umbilicus, low spire (last whorl comprising more than 90% of shell height), and obsolete spiral cords on the upper part of the last whorl. Grooves between five cords below the pseudolivid groove end in sharp crenulations at the outer lip. In my material from Little Stave Creek, Alabama, most individuals have a relatively restricted callus, but one large individual (height 34.1 mm) has the spire nearly obliterated by a massive callus deposit. *Sulcobuccinum carinatum* and *S. perspectivum* are related species with an open umbilicus. Although Palmer (1937) regarded them as forms of *vetustum*, my examination of this group reveals subtle but consistent differences. *Sulcobuccinum carinatum* from the Stone City and Cook Mountain Formations of Texas (Middle Eocene) and *S. perspectivum* from the Moodys Branch Formation of Mississippi (Late Eocene) are somewhat higher-spired (last whorl comprising 81 to 83% of shell height) than is *S. vetustum*. The last whorl of *S. carinatum* is somewhat less slender (whorl diameter-to-whorl height ratio 0.93) than that of *S. perspectivum* (ratio 0.86), but the shell of *S. carinatum* has a somewhat more slender appearance because the widest point of the last whorl lies at a relatively lower position and because the shoulder is less wide than the periphery in *S. carinatum*. Other species in this group include *S. linosum*, *S. nanum*, and *S. santander* from the Gulf Coastal Plain, and the nonumbilicate *S. obtusum* from France. Dockery (1980) speculates that the thick callus deposits of *S. santander* from the Bashi Marl Member of the Hatchetigbee Formation (early Eocene) of Mississippi indicate a gravitationally stable shell in a wave-swept, shallow-water environment. Similar callus deposits are developed in cooccurring species of *Ancillopsis* and in several volutid gastropods.

Vermeij and DeVries (1997) reviewed a group of large (height up to 50 mm), nonumbilicate, smooth species from Peru, in which the outer lip is adapically extended beyond the tip of the spire in mature shells. This group, which may have extended into the Early Oligocene (T. J. DeVries, personal communication), includes *P. retusum* and its subspecies *S. r. samanicum* and *S. r. mancorense*, as well as *S. vientoense* and a form comparable to *S. retusum* from Colombia and Curaçao (see also Clark & Durham, 1946; Jung, 1974).

One species of the smooth *Buccinorbis* phenotype is known from Japan. Although originally described as a species of *Orthaulax* by Nagao (1924), the affinities of *S. japonicum* with *Pseudoliva* were recognized by Nagao (1928) by virtue of the presence of a pseudolivid groove. Honda (1991, 1994) records this species, in which axial sculpture is absent and spiral sculpture is confined to the zone below the pseudolivid groove, from Late Eocene (Takashiman and Okinoshiman) and Early Oligocene (Mazean and Funazuan) deposits.

Genus *Hubachia* Etayo Serna, 1979
(Figure 4)

Type species: *Hubachia ramirolobae* Etayo Serna, 1979, by original designation.

Diagnosis: Shell medium-sized, maximum height about 30 mm, ovate; protoconch unknown; spire moderately low to very low, last whorl comprising 81 to 100% of total shell height; last whorl marked by low, sharply angulate shoulder, immediately below which is a deep spiral groove; between upper groove and pseudolivid groove, last whorl evenly rounded; base of last whorl not constricted; spiral sculpture consisting of fine spiral threads on spire whorls, and of eight weak cords below pseudolivid groove on last whorl; axial sculpture confined to spire whorls, consisting of about 15 irregular, rounded, low ribs; pseudolivid groove situated high on last whorl, just below its middle; outer lip unknown; aperture broadly ovate, its height-to-breadth ratio approximately 2.0; columellar and parietal callus thick, well developed ventrally, but not extending onto spire; umbilicus absent.

Stratigraphic and geographic distribution: Paleocene, Colombia.

Discussion: Etayo Serna (1979:37) introduced *Hubachia* as a monotypic genus of the family Olividae from the Paleocene of Colombia. He noted that *Hubachia* differs from the olivid genus *Olivancillaria* d'Orbigny, 1839, by having axial sculpture on the spire whorls and by having basal cords on the basal half of the last whorl. Etayo Serna (1979) also noted the presence of a pseudolivid groove, and remarked on the similarity of *Hubachia* to *Pseudoliva*, from which it differs by the presence of axial sculpture on the spire whorls.

Poor preservation of the available specimens precludes detailed comparison with other genera, and forces me to consider the assignment and status of *Hubachia* as provisional. The very deep spiral groove immediately below the sharply angled shoulder distinguishes *Hubachia* from other pseudolivid genera. *Hubachia* has an unusually broad aperture and low spire, and has a rounded periphery well below the shoulder. It superficially resembles some species of *Sulcobuccinum* in having axial sculpture confined to the spire whorls, but diverges from species of *Sulcobuccinum* in which axial sculpture is absent on the last whorl by the sharp shoulder and accompanying groove.

Hubachia differs from *Sulcobuccinum* by having axial sculpture confined to the early teleoconch whorls, by the exceptionally low spire, and by the presence of a very deep groove just below the sharply angulate shoulder. The periphery of the last whorl is evenly rounded in *Hubachia*. The aperture of *Hubachia* is relatively very broad compared to that in species of *Sulcobuccinum* and *Buccinorbis*. *Hubachia* differs further from *Buccinorbis* by the character of the shoulder and its accompanying groove.

Genus *Benthobia* Dall, 1889

Type species: *Benthobia tryonii* Dall, 1889, by original designation.

Synonym:

Nux Barnard, 1960 [Type species: *Nux alabaster* Barnard, 1960 (= *Benthobia triennia* Dall, 1889)].

Diagnosis: Shell small, maximum height 13 mm, thin; protoconch multispiral; spire moderately low, last whorl comprising 75 to 77% of total shell height; last whorl inflated, evenly rounded above, not constricted basally; spiral sculpture obsolete; axial sculpture consisting of numerous very fine, short riblets confined to subsutural ramp and shoulder; pseudolivid groove very shallow, situated just below middle of last whorl; outer lip with obsolete labral tooth; inner side of outer lip smooth; posterior notch absent; aperture ovate, its height-to-breadth ratio 2.0 to 2.3; columellar and parietal callus thin, of very limited extent; parietal ridge absent; siphonal fasciolar ridge absent; anterior siphonal notch obsolete; umbilicus absent.

Stratigraphic and geographic distribution: Recent, bathyal and abyssal eastern and western Atlantic Ocean from 38°N to 33°S; southwestern Indian Ocean; off New Zealand; 800 to 4380 m.

Discussion: Dall (1889:131) originally placed his new genus *Benthobia* in the family Cancellariidae because of its superficial resemblance to *Admete* Kroyer *in* Moller, 1842; but he expressed doubts about this assignment in view of the absence of anatomical information. The absence of columellar folds also implied that *Benthobia* was unlikely to belong to the Cancellariidae. Bouchet and Warén (1985) figured the radula of *Benthobia* and transferred the genus to the olivid subfamily Pseudolivinae. Kantor's (1991) anatomical work subsequently provided further support for this reassignment.

As presently understood, *Benthobia* is a monotypic genus of Recent bathyal and abyssal gastropods. Anatomically, *Benthobia* is plesiomorphic in having the radular sac situated at the base of the proboscis and by retaining the connection between the radular retractor muscle and columellar muscle (Kantor, 1991).

Among living Pseudolividae, *Benthobia* is unique in having a multi-spiral protoconch, which Bouchet and Warén (1985) link to planktotrophic development. This character is shared with the Paleocene genus *Fusopsis*. *Benthobia* and *Fusopsis* have many features in common, and further work may indicate that *Fusopsis* represents an early appearance of *Benthobia*. Both genera have axial sculpture confined to the upper part of the whorl. *Fusopsis* differs from *Benthobia* mainly by having a slightly constricted base.

Another similar genus is *Fusulculus*, which like *Benthobia* has a very shallow anterior siphonal notch. Both genera lack a posterior notch and parietal rib. *Fusulculus* differs from *Benthobia* by being basally constricted. The spire of *Fusulculus* is higher, and spiral sculpture is well developed on the base. *Fusulculus* bears a small but distinct labral tooth as well as several crenulations below the tooth on the outer lip, whereas in *Benthobia* the tooth is obsolete and crenulations are absent.

The genus *Zemira* resembles *Benthobia* in lacking a fasciole and basal constriction and in having a very shallow anterior siphonal notch. It differs by having well developed spiral sculpture, by possessing a distinct labral tooth, and (in the type species) by lacking any trace of axial sculpture.

Genus *Fusopsis* Ravn, 1939.

Type species: *Pseudoliva (Fusopsis) canalifera* Ravn, 1939.

Diagnosis: Shell very small, maximum height 3.5 mm, relatively high-spired; last whorl comprising 70% of shell height; protoconch multispiral; shell fusiform, constricted at base of last whorl; teleoconch whorls convex, separated by deep, canaliculate suture; spiral sculpture consisting of 10 threads on last whorl; axial sculpture consisting of 12 riblets on upper part of last whorl; pseudolivid groove situated just below middle of last whorl, forming small labral tooth at edge of outer lip; umbilicus lacking (surmised from description of type species by Ravn, 1939).

Stratigraphic and geographic distribution: Paleocene of Denmark.

Discussion: Ravn (1939:76) introduced *Fusopsis* as a subgenus of *Pseudoliva* in the course of describing *Pseudoliva canalifera* from the Paleocene of Copenhagen, Denmark. Although he did not provide a diagnosis for the subgenus, he made it clear that *Fusopsis* differs from

Pseudoliva s.s. by having a multispiral rather than a paucispiral protoconch. Ravn (1939) was apparently unaware of the genus *Benthobia,* which like *Fusopsis* has a multispiral protoconch, but which was then classified in the Cancellariidae.

Without the protoconch, *Fusopsis* would be indistinguishable from other relatively high-spired species of small, Paleocene pseudolivids that I assign here to the genus *Sulcobuccinum.* In fact, Ravn (1939) pointed out that *Pseudoliva koeneni* Ravn, 1939, which co-occurs with *Fusopsis canalifera,* is transitional to more typical "*Pseudoliva*" (= *Sulcobuccinum* as used in this paper). *Fusopsis canalifera* differs from most species of *Sulcobuccinum* by being basally slightly constricted. It is possible that several species here tentatively assigned to *Sulcobuccinum* will prove to belong to *Fusopsis,* which, as discussed under *Benthobia,* may itself fall as a junior synonym of *Benthobia.*

Genus *Sulcoliva,* new genus
(Figures 8–9)

Type species: *Pseudoliva monilis* Olsson, 1928.

Diagnosis: Shell moderately small, maximum height 27.4 mm, narrowly ovate to biconic; protoconch unknown; spire high, last whorl comprising 59 to 75% of total shell height; sutures appressed; rounded above, slightly or not constricted basally; spiral sculpture consisting of 14 to 16 weak threads below pseudolivid groove on last whorl; axial sculpture consisting of 20 to 25 low, weak beads on periphery of last whorl, not visible on spire whorls; pseudolivid groove at high position on last whorl, expressed as stepwise basal narrowing rather than as a groove; outer lip with small labral tooth; posterior notch weak; aperture elongate-ovate, its height-to-breadth ratio 2.4 to 3.0; columellar and parietal callus of very limited extent; siphonal fasciolar ridge low, rounded; anterior siphonal notch deep; umbilicus absent.

Stratigraphic and geographic distribution: Early to Late Eocene, Peru.

Included species: *Pseudoliva monilis* Olsson, 1928; *Pseudoliva modesta* Olsson, 1928.

Discussion: I propose the new genus *Sulcoliva* for two unusual pseudolivids from the Eocene of Peru described by Olsson (1928). *Sulcoliva* resembles *Sulcobuccinum,* but is distinguished by the high spire and by the presence of a peripheral band of fine beads. In *Sulcobuccinum,* axial sculpture, when present, normally extends from the suture to a point above the pseudolivid groove; whereas in *Sulcoliva* the axial riblets are confined to the periphery and cannot be seen on the spire whorls. Moreover, whereas the pseudolivid groove in *Sulcobuccinum* is deep, that of *Sulcoliva* has an adapical but not an abapical edge. The groove is therefore more like a step, a sudden, very slight abapical narrowing of the whorl at or just below mid-whorl height. *Sulcoliva* also resembles the Recent genus *Naudoliva.* Both genera have a high-spired shell with an ill-defined pseudolivid groove and a distinct labral tooth. *Naudoliva* differs from *Sulcoliva* by lacking axial sculpture and by the absence of a posterior notch.

The genus *Sulcoliva* contains two species from the Eocene of northern Peru. These are *S. monilis,* the type species, from the Parinas Sandstone (Early Eocene), and the higher-spired, somewhat larger *S. modesta* from Olsson's (1930) Talara Formation (Late Eocene, Bartonian).

Genus *Naudoliva* Kilburn, 1989

Type species: *Naudoliva caitlinae* Kilburn, 1989, by original designation.

Diagnosis: Shell thin, ovate, of medium size, maximum height 29 mm; protoconch paucispiral; spire relatively high, last whorl comprising 64% to 69% of total shell height; suture appressed or impressed; last whorl with concave subsutural ramp, a rounded or weakly angulated shoulder, and an unconstricted base; spiral sculpture consisting of very fine threads on spire whorls and on base of last whorl; axial sculpture absent (*N. caitlinae*) or consisting of short, rounded ribs at shoulder above periphery (*N. vorsteri*); outer lip planar, with long labral tooth; inner side of outer lip smooth; posterior notch absent; aperture elongate-ovate, its height-to-breadth ratio about 2.7; columella and parietal callus thin, not extensive; columella without fold at base; parietal rib absent; siphonal fasciole low, rounded, sculptured with very fine spiral threads; umbilical slit very narrow or absent; anterior notch deep; periostracum absent.

Stratigraphic and geographic distribution: Late Miocene, Trinidad; Recent, Indian Ocean coast of South Africa.

Discussion: Kilburn (1989) proposed *Naudoliva* to accommodate *N. caitlinae,* a distinctive pseudolivid characterized by a high spire, small umbilical slit, and very fine spiral but no axial sculpture. The shell has an unusually long labral tooth, situated at the end of shallow, broad pseudolivid groove on the lower third of the last whorl. There is no periostracum. Kilburn noted that the radula has a unicuspidate lateral plate, as in *Benthobia* (Kantor, 1991), and that the head tentacles are bilobed, as in *Luizia zebrina* (Kantor, 1991). *Pseudoliva,* by contrast, has a bicuspidate lateral plate and single head tentacle. The latter character also occurs in *Zemira* (see Ponder & Darragh, 1975; Kantor, 1991). The absence of a posterior notch on the outer lip is a character that *Naudoliva* has in common with *Benthobia* and *Fusulculus. Naudoliva* differs from these genera by having a long labral tooth, deep anterior siphonal notch, and a low but distinct siphonal fasciole. It differs from *Luizia* by having a smooth instead of lirate inner side of the outer lip, and by lacking a posterior notch.

The type species, *N. caitlinae,* is from Transkei, South Africa. Its shell is very slightly constricted at the base,

and lacks axial sculpture. *Naudoliva vorsteri*, recently described by Lussi (1995) from Algoa, Bay, differs from *N. caitlinae* by lacking the basal constriction and by having about ten short axial ribs at the shoulder. These ribs do not extend up to the suture or down to the gently rounded periphery, and become obsolete near the outer lip. The absence of the periostracum characterizes both species, and readily distinguishes this unusual genus from other South Africa pseudolivid (see also Lussi, 1995).

Mansfield (1925) described *Pseudoliva guppyi* on the basis of a single, exquisitely preserved specimen from the Springvale Formation (Late Miocene) of Trinidad. My examination of the holotype reveals that the shell is moderately high-spired, the last whorl comprising 73% of total shell height. The last whorl is not constricted at the base; it is sculptured by very faint spiral threads, and below the pseudolivid groove by more prominent spiral cords. The low shoulder is marked by sixteen short, weak axial ribs. The shallow pseudolivid groove is situated just below the middle of the last whorl, and ends in a relatively long, sharp labral tooth. The inner side of the outer lip is smooth. The aperture is ovate, its height-to-breadth ratio being about 2.3. A posterior notch, parietal rib, siphonal fasciole, and umbilicus are lacking. The anterior siphonal notch is deep.

I assign Mansfield's species provisionally *Naudoliva*. It is very similar in form and sculpture to *N. vorsteri*, from which it differs in having a larger number of axial ribs (sixteen versus ten), a broader aperture (apertural height-to-breadth ratio 2.3 instead of 2.7), and a smaller shell (10.4 versus 29.4 mm). The only significant feature of *Pseudoliva guppyi* that is inconsistent with assignment to *Naudoliva* is the absence of a siphonal fasciole, which is low and weak in *Naudoliva*. In the absence of a fasciole, *P. guppyi* resembles *Fusulculus*, with which it additionally has in common the numerous short axial riblets and the absence of a posterior notch. *Pseudoliva guppyi* differs from *Fusulculus*, however, in not being constricted at the base, in having a long labral tooth, a much deeper siphonal notch, a relatively broader aperture, and a shorter spire. It is possible that the absence of a siphonal fasciole in the Miocene fossil as well as in species of *Fusulculus*, *Benthobia*, and *Zemira* is a juvenile or neotenic feature. For now, it seem best to assign *Pseudoliva guppyi* to *Naudoliva*, despite the great geographic distance between Trinidad and the South African localities where the other two species of *Naudoliva* occur.

Naudoliva guppyi is only one of two pseudolivids known from the tropical western Atlantic Neogene, the other being *Macron constrictus* from the early Miocene of Venezuela. As noted by Mansfield (1925), there is no living or fossil tropical American species that is even remotely similar to this unusual late Miocene species from Trinidad.

Genus *Luizia* Douvillé, 1933

Type species: *Buccinum (Luizia) costae* Douvillé, 1933, by original designation.

Diagnosis: Shell small, maximum height 22 mm; ovate; protoconch paucispiral; sutures appressed; spire moderately high, last whorl comprising 77 to 83% of total shell height; last whorl shouldered above, not constricted basally; spiral sculpture consisting of very fine threads over whole shell surface; axial sculpture consisting of 14 to 17 riblets on upper part of whorl, forming nodes at shoulder; pseudolivid groove situated high on last whorl, about one-third the distance from the anterior end of the shell; outer lip planar, with small, distinct labral tooth; inner side of outer lip with 11 to 12 lirae; posterior notch shallow; aperture narrowly elongate, its height-to-breadth ratio 3.3; columellar and parietal callus thin, of very small extent; parietal rib absent; siphonal fasciole bounded posteriorly by low keel; anterior notch deep; umbilicus absent.

Stratigraphic and geographic distribution: Early? Miocene to Recent, Angola.

Discussion: Douvillé (1934) proposed *Luizia* as a subgenus of *Buccinum* for a small gastropod from the Miocene (probably Burdigalian, Early Miocene) of Angola. Although he noted the presence of a pseudolivid-like groove on the lower part of the last whorl, Douvillé (1934) assigned *Luizia* to *Buccinum* because of its weak axial riblets and spiral threads. In the Recent fauna, *Luizia* is represented by *Pseudoliva zebrina* A. Adams, 1855, from Angola (Figure 13–15). This species has a small shell (maximum height 19.2 mm) with a relatively high spire (last whorl comprising 77 to 83% of total shell height), 14 to 17 weak axial riblets forming nodes at the shoulder crossed by very weak threads. The inner side of the outer lip bears 11 to 12 weak lirae.

The genus *Luizia* closely resembles *Naudoliva*, *Fusulculus*, and slender species of *Sulcobuccinum*. It differs from all these by having the inner side of the outer lip lirate (sculptured by small riblets) instead of smooth. *Luizia* differs from *Fusulculus* and *Naudoliva* by having a weak posterior notch, and from *Fusulculus* by the presence of a siphonal fasciole and by lacking a basal constriction on the last whorl.

Genus *Fusulculus* Bouchet & Vermeij, 1998

Type species: *Fusulculus crenatus* Bouchet & Vermeij, 1998, by original designation.

Diagnosis: Shell relatively small, maximum height 18.4 mm, fusiform; protoconch paucispiral; sutures appressed; spire relatively high, last whorl comprising 61 to 67% of total shell height; last whorl with concave subsutural ramp, a rounded shoulder, and basal constriction; spiral sculpture consisting of up to 15 weak cords between shoulder and base, sometimes obsolete; axial sculpture consisting of 14 to 16 riblets extending from the suture to a point just below the shoulder; pseudolivid groove at lip convex ventrally, with very weak labral tooth and five weak basal crenulations; inner side of outer lip smooth; posterior notch obsolete; aperture narrowly

ovate, its height-to-breadth ratio 2.6 to 3.2; columellar and parietal callus thin, of very limited extent; parietal rib absent; siphonal fasciole and umbilicus absent; anterior notch shallow.

Stratigraphic and geographic distribution: Recent, bathyal southwestern Pacific from Coral Sea and New Caledonia to north of New Zealand.

Discussion: The genus *Fusulculus* resembles *Benthobia* and *Zemira* in having a very shallow anterior siphonal notch, a limited extent of callus, a high position of the pseudolivid groove on the last whorl, and in lacking a parietal rib at the adapical end of the inner lip. *Fusulculus* differs from these genera by being constricted at the base, and from the type species of *Zemira* by having well developed axial sculpture. *Naudoliva* and *Fusulculus* have in common the absence of a posterior notch on the outer lip, but *Fusulculus* is distinctly constricted at the base, whereas *Naudoliva* has little or no basal constriction. Moreover, *Naudoliva* has a low, rounded siphonal fasciole and a deep siphonal notch, features lacking in *Fusulculus*.

Bouchet and Vermeij (1997) describe two species, *F. crenatus* and *F. albus*, from bathyal waters in the southwestern Pacific. These species are the only pseudolivids living in the tropical Indo-West Pacific.

Genus *Zemira* H. & A. Adams, 1853

Type species: *Eburna australis* G. B. Sowerby, 1833, by monotypy.

Synonym:

Eburnopsis Tate, 1889 (type species: *Eburnopsis aulacoessa* Tate, 1889, = *Zemira australis*, *fide* Ponder & Darragh, 1975)

Diagnosis: Shell relatively small, maximum height 21 mm, ovate; protoconch paucispiral; spire moderately high, last whorl comprising 66 to 68% of total shell height; sutures deeply channeled; last whorl rounded above, not constricted basally; spiral sculpture consisting of as many as 25 weak flattened cords between suture and base of last whorl, the six to seven cords below pseudolivid groove widest; axial sculpture absent; pseudolivid groove situated high on last whorl, just below its midpoint; outer lip with distinct labral tooth and basal crenulations; inner side of outer lip smooth; posterior notch present; aperture ovate, its height-to-breadth ratio 1.9 to 2.2; columellar and parietal callus thin, of very limited extent; parietal rib absent; siphonal fasciole absent; anterior siphonal notch obsolete; umbilicus usually absent.

Stratigraphic and geographic distribution: Late Eocene to Recent, Australia.

Discussion: Ponder and Darragh (1975) have fully reviewed the living and fossil species of *Zemira* and provided anatomical details for the two living species, *Z. australis* (northern New South Wales to Tasmania) and *Z. bodalla* (southern Queensland). H. & A. Adams (1853) proposed *Zemira* as a member of the muricid subfamily Purpurinae because of characters of the radula. Fischer (1884) regarded *Zemira* as a section of *Macron* in the Buccinidae. Cossmann (1901) assigned it to the buccinid subfamily Latrunculinae (= Babyloniinae). Ponder and Darragh's (1975) anatomical work revealed similarities to *Pseudoliva*, and suggested that the radular similarities with Purpurinae (= Ocenebrinae and Rapaninae) result from inheritance of plesiomorphic character states (see also Kantor, 1991).

Zemira resembles *Fusulculus* in its relatively high spire, position of the pseudolivid groove, lack of a siphonal fasciole, and obsolete anterior notch. It differs from *Fusulculus* by lacking the basal constriction, by having a deeply channeled suture, and by lacking axial sculpture in most species. The labral tooth is distinct in *Zemira* but obsolete in *Fusulculus*. *Zemira* differs from *Benthobia* by having a higher spire, a much less inflated last whorl, well-developed spiral sculpture, a posterior notch, and a labral tooth. Axial sculpture, which is present as short riblets on the upper part of the whorl in *Benthobia*, is lacking in *Zemira* .

The type species of *Zemira* , *Z. australis*, is interpreted by Ponder and Darragh (1975) as a long-ranging, variable species. It includes *Eburnopsis aulacoessa* Tate, 1889 and *Zemira praecursoria* Tate, 1888, which are heavily corded and smooth forms respectively from the Balcombian (middle Miocene) of Victoria. The spire of *Z. australis* is generally higher than in other species of the genus. Axial sculpture is absent in *Z. australis* and in its presumed progenitor, *Z. australis antecursoria*, from the Longfordian and Batesfordian (early Miocene) of Victoria; but it is present in *Z. tessellata*, the Late Oligocene ancestor of the *Z. australis* lineage from the Jan Juc Formation of Victoria (Ponder & Darragh, 1975). An umbilicus is absent in *Z. a. australis*, but is variably developed in the other species assigned by Ponder and Darragh (1975) to *Zemira* . The earliest representative of *Zemira* recognized by Ponder and Darragh (1975) is an undescribed species from the Glen Aire Clay (Late Eocene) of Victoria. This species lacks axial sculpture and has a wide umbilicus.

Genus *Testallium* Vermeij & DeVries, 1997.

Type species: *Gastridium cepa* Sowerby, 1846, by original designation.

Synonyms:

Gastridium Sowerby, 1846 (type species: *Gastridium cepa* Sowerby, 1846), *non* Modeer, 1793, *nec* Sowerby, 1842.

Diagnosis: Shell large, maximum height 57 mm, broadly fusiform; protoconch unknown; last whorl rounded or shouldered above, constricted basally; spiral sculpture variably expressed, consisting of cords that are strongest below pseudolivid groove; axial sculpture usually absent, or when present is confined to spire whorls (*T. voluta*); pseudolivid groove at low position on last whorl; outer lip planar, with distinct labral tooth and

about five basal crenulations; posterior notch present; aperture ovate, its height-to-breadth ratio 1.9 to 2.4; columellar and parietal callus of limited extent but may be thick; parietal rib present; siphonal fasciole strong, bounded above by prominent keel; anterior notch deep; umbilicus present or absent.

Stratigraphic and geographic distribution: Early Miocene to Late Pliocene, temperate western South America.

Discussion: Vermeij and DeVries (1997) have given a full account of the synonymy and composition of the genus *Testallium* from the Miocene and Pliocene of temperate western South America. The name *Gastridium* Sowerby, 1846, which has been used previously for these species (Sowerby, 1846; Philippi, 1887; Herm, 1969), is preoccupied by *Gastridium* Modeer, 1793 (Conidae) and *Gastridium* Sowerby, 1842 (a synonym of *Pseudoliva*). Von Ihering (1907) referred species of Sowerby's (1846) *Gastridium* to *Austrocominella* von Ihering, 1907, which he proposed as a subgenus of *Cominella* Gray, 1850. Allmon (1990) and Beu & Maxwell (1990) have pointed out that *Cominella (Austrocominella) fuegensis* von Ihering, 1907, the type species of *Austrocominella* from the Rio Turbio and Loreto Formations (Early? Miocene of Tierra del Fuego), is closely related to or belongs in the same genus as does *Zelandiella subnodosa* (Hutton, 1877), the type species of *Zelandiella* Finlay, 1926, from the Altonian (Early Miocene) of New Zealand. Von Ihering (1907) mistakenly believed that the South American species of *Gastridium* Sowerby, 1846, lack a pseudolivid groove. The inclusion of these species in *Austrocominella*, which indeed does lack a pseudolivid groove, was therefore unwarranted. Species of *Gastridium* have also occasionally been confused with members of the ocenebrine muricid genus *Chorus* Gray, 1847 (type species: *Chorus giganteus* (Lesson, 1831)), from Chile. Both genera have a labral tooth corresponding to a basal groove, but *Chorus* lacks the posterior notch and parietal rib characteristic of *Testallium*, the replacement name for *Gastridium* Sowerby, 1846. In *Chorus* as in other muricids, the spiral sculpture of the last whorl increases in prominence from the base to the shoulder rather than from the shoulder to the base as in *Testallium* and other pseudolivids. The cords of *Chorus* are widely separated and rounded, not crowded as in *Testallium*.

Testallium differs from *Pseudoliva* by having the last whorl covered with fine spiral sculpture instead of being smooth, by having the base of the last whorl distinctly constricted (that is, with a concave lateral profile) instead of being evenly tapered, by having a prominent, keel-like siphonal fasciole instead of a low, rounded one, by the very limited development of callus, and by having the lower part of the outer lip distinctly crenulated. It differs from *Sulcobuccinum* by the lower position of the pseudolivid groove on the last whorl, by the limited development of callus, and by the presence of a parietal rib at the adapical end of the inner lip. *Testallium* is very similar to *Macron*. Whereas the inner side of the outer lip of *Testallium* is smooth, that of *Macron* is sculptured with riblets (lirae).

There is considerable intraspecific variation in the degree of development of the shoulder. In some forms of *T. cepa* and in *T. voluta*, the shoulder may be developed as a raised ridge in the mature shell; whereas in other specimens of *T. cepa*, the upper part of the whorl is rounded (see Vermeij & DeVries, 1997).

Included in *Testallium* are *T. cepa* from the Early Miocene of southern Peru to southern Chile, *T. voluta* from the Heath Formation (?Early Miocene) of northern Peru, and *T. escalonia* from the Late Pliocene of Chile. *Testallium voluta*, which Olsson (1932) originally described as a species of *Acanthiza (Chorus)*, differs from the other two species by having axial ribs on the spire whorls. Olsson's *Acanthiza* was presumably a misspelling of *Acanthina*, another ocenebrine muricid genus with a labral tooth (see Vermeij & DeVries, 1997).

Genus *Macron* H. & A. Adams, 1853

Type species: *Pseudoliva (Macron) kellettii* A. Adams, 1854 (= *Buccinum aethiops* Reeve, 1847).

Synonym:
Macroniscus Thiele, 1929 (Type species: *Macron lividus* A. Adams, 1855).

Diagnosis: Shell small to large, maximum height 20 to 100 mm, ovate; protoconch paucispiral; spire relatively high, last whorl comprising 68 to 74% of total shell height; sutures appressed to deeply impressed; last whorl rounded or shouldered above, little or not constricted basally; spiral sculpture consisting of weak to very prominent cords decreasing in strength from base to shoulder; axial sculpture absent; pseudolivid groove situated low in last whorl; outer lip planar, usually with distinct labral tooth (obsolete in *M. lividus*), strongly crenulated below; inner side of outer lip lirate; posterior notch weak; aperture ovate in most species, its height-to-breadth ratio 1.9 to 4.1 (narrowly elongate in *M. merriami*); columella with weak fold at entrance of siphonal canal; columellar and parietal callus of very limited extent; siphonal fasciole prominent, bounded above by keel; anterior notch deep; umbilicus present or absent.

Stratigraphic and geographic distribution: Early Miocene to Recent, warm-temperate northeastern Pacific; ?Early Pliocene, Japan.

Discussion: *Macron* has remained a taxonomic enigma ever since H. & A. Adams (1853:132) introduced it as a subgenus of *Pseudoliva* in the muricid subfamily Purpurinae. Adams (1855) and Sowerby (1859) maintained this assignment. Fischer (1884) referred *Macron* to the Buccinidae, along with other Pseudolividae. Cossmann (1901) and Melvill (1903) refined this assignment by referring the genus to the Latrunculinae or Eburninae (= Babyloniinae), and noted that, whereas *Macron* has an unguiculate operculum with a terminal nucleus, *Pseudoliva* has a purpuroid operculum with a laterally

placed nucleus. Grant and Gale (1931) re-examined the operecula of the two genera and concluded that both are characterized by a terminal opercular nucleus. They therefore reaffirmed the close relationship between *Macron* and *Pseudoliva*. Thiele (1929) described the radula of *M. trochlea* (Gray) (= *M. aethiops*) and of *M. lividus*, and assigned the genus to the Buccinidae. In this assignment, he was followed by Wenz (1938–44), Glibert (1963), Addicott (1970), Keen (1971), and Abbott (1974).

Yuri Kantor (personal communication) suggests that the radula of *Macron* is very similar to that of the Nassariidae. As illustrated by Thiele under the name *M. trochlea*, the rachidian tooth is multicuspidate with small cusps, and the lateral teeth are tricuspidate. The pseudolivid radula, by contrast, either has a multicuspidate rachidian and unicuspidate marginal teeth or a tricuspidate rachidian with very large cusps and bicuspidate marginal teeth (Kantor, 1991). The shell characters of *Macron*, however, differ widely from those of Nassariidae. The genus *Nassarius* Dumeril, 1906, and related taxa (see Cernohorsky, 1984) are characterized by determinate growth, and by a polished outer lip with an anterior sinus. *Macron*, by contrast, has a simple, sharp-edged, outer lip indicating indeterminate growth and lacking any trace of an anterior sinus.

The pseudolivid affinities of *Macron* are strongly supported by shell characters. These include a thick periostracum, pseudolivid groove and corresponding labral tooth (obsolete in *M. lividus*), sharp-edged simple outer lip, posterior notch, and spiral sculpture most strongly expressed near the base. The only similar genus that has traditionally been referred to the Buccinidae is *Triumphis*, which differs from *Macron* chiefly by the absence of the pseudolivid groove and labral tooth. With the transfer of *Triumphis* to the Pseudolividae (see below), there is no other buccinid genus that closely resembles *Macron*.

Macron is most similar to *Testallium*, from which it differs principally in having the inner side of the outer lip sculptured by nine to seventeen riblets (lirae). In *Testallium*, the inner side of the outer lip is smooth.

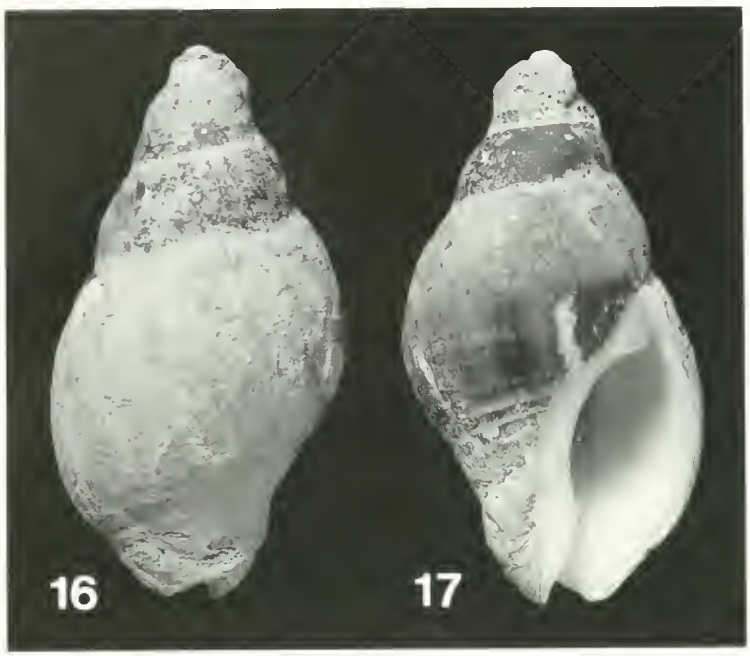
The middle Miocene species *Macron merriami* from the Temblor Formation of southern California may represent an evolutionary link with *Testallium*. This species has very weak spiral sculpture, a rounded (not shouldered) last whorl, appressed suture, weakly constricted base, and an unusually narrow aperture (height-to-breadth ratio 4.1). Because the aperture of the holotype is filled with matrix, the presence of lirae on the inner side of the outer lip cannot be ascertained. The species could therefore be assigned to either *Testallium* or *Macron*. I retain it in *Macron* on the basis of its geographic provenance (California instead of western South America).

Another species, *Macron hartmanni*, may link *Macron* with the genus *Triumphis*. This species, described by Hertlein and Jordan (1927) from the San Ignacio Formation (middle to late Miocene; see Smith, 1984) of Baja California Sur, Mexico, resembles *Triumphis* in having a raised, keel-like shoulder, but differs from that genus by having six to ten low, flattened cords on the last whorl and by the presence of a blunt but distinct labral tooth at the end of a pseudolivid groove. Addicott (1970) provisionally assigned *M. hartmanni* to *Nicema*, a taxon that has occasionally been considered a subgenus of *Triumphis* but that is here assigned to the buccinid subfamily Photinae (see below). *Nicema* lacks the labral tooth and pseudolivid groove of *Macron*. I therefore agree with Hertlein and Jordan (1927) that their species should be referred to the genus *Macron*.

The type species of *Macron*, *M. aethiops*, is the largest, most heavily sculptured living member of the Pseudolividae, attaining a height of 100 mm. The expression of spiral sculpture above the pseudolivid groove is highly variable even within populations. In typical *M. aethiops*, seven thick, flattened or rounded cords with very deep interspaces lie between the pseudolivid groove and the shoulder. In the *kellettii* form, only the lowest one or two of these cords are expressed. All forms have a deeply impressed, canaliculate suture, and all have fifteen or more lirae on the inner side of the outer lip. In the living fauna, *M. aethiops* occurs on the Pacific coast of Baja California from just south of Ensenada to just south of Bahia Magdalena. There appears to be a geographically isolated population in the Gulf of California. The species is not represented on the southern part of the Baja California peninsula. My examination of a specimen reported by Mulliner (1996) from Isla Danzante in the Gulf of California indicates that this specimen falls well within the limits of variation of the species as a whole. With only one cord above the pseudolivid groove, the specimen from Isla Danzante belongs to the *kellettii* form of *M. aethiops*. It is unusual among pseudolivids in that the left (leading) edge of the inner lip has a distinct margin. In the fossil record, *M. aethiops* occurs in the lower Olcese sand (middle Miocene) and the San Pedro beds (Early Pleistocene) of southern California (Grant & Gale, 1931; Addicott, 1970).

Thiele (1929) proposed the subgenus *Macroniscus* for *Pseudoliva* (*Macron*) *livida* A. Adams, 1855, a small species from the Pleistocene and Recent of southern California. It differs from other species of *Macron* by its small size (maximum height 18.6 mm), appressed rather than channeled suture, obsolete pseudolivid groove and labral tooth, and very weak basal spiral cords. Although *M. lividus* does not closely resemble the large, strongly sculptured *M. aethiops*, several species are morphologically intermediate. These include *M. orcutti*, *M. mcleani* n. sp. (see below), and an early Miocene species, *Macron constrictus*, described by Gibson-Smith, Gibson-Smith, and Vermeij (1997) from the Cantaure Formation of Venezuela. This less sculptured group does not merit distinction as a subgenus or genus *Macroniscus*, which I therefore consider a subjective synonym of *Macron*.

Besides the living and fossil species of *Macron* from the warm-temperate northeastern Pacific and the early Miocene species from Venezuela in the western Atlantic,



Figures 16–17. *Macron mcleani* new species; Bahia Gonzaga, Gulf Coast, Baja California Norte, Mexico; LACM 37-119. Shell height 23.1 mm.

there is one species from the early Pliocene of Japan that has been tentatively referred to *Macron*. Chinzei (1959) named "*Macron*" *nipponensis* on the basis of a single, thick-shelled specimen from the Kubo Formation of Honshu. It is characterized by thirteen spiral cords on the last whorl and five cords on spire whorls, the cords increasing in strength toward the constricted base. Chinzei (1959) mentions neither a pseudolivid groove nor a labral tooth. The outer lip, whose inner side is ornamented with ten denticles, is exceptionally thick and is posteriorly notched. An umbilicus is absent. "*Macron*" *nipponensis* differs from *Macron* by the absence of a labral tooth and pseudolivid groove and by the presence of denticles rather than brief lirae on the inner side of the outer lip. If the species belongs to the Pseudolividae, it may have paralleled *Triumphis* in having lost the pseudolivid groove and labral tooth.

For the time being, I retain *M. nipponensis* in the genus *Macron*.

Macron mcleani, new species
(Figures 16–17)

Diagnosis: *Macron* with smooth, rounded whorl, appressed suture, nine lirae on inner side of outer lip, narrow aperture, and fibrous periostracum.

Description: Shell ovate-fusiform, consisting of about five teleoconch whorls; spire moderately high, last whorl comprising 68% of total shell height; suture appressed; last whorl gently and evenly rounded on upper part, very weakly constricted at base; spiral sculpture consisting of three low cords on base, above which is a distinct (pseudolivid) groove; axial sculpture absent; outer lip planar, with three strong crenulations on anterior sector below a blunt labral tooth; inner side of outer lip with nine brief lirae; posterior end of aperture with parietal rib; inner lip appressed, with a distinct fold at entrance of siphonal canal; aperture elongate, its height-to-breadth ratio 3.1; siphonal fasciole low, rounded; anterior siphonal notch deep; umbilicus absent; periostracum fibrous; shell brown, interior of aperture white.

Holotype: Height 23.1 mm, diameter 11.9 mm, aperture height 15.6 mm, aperture width 5.1 mm. LACM 2812.

Type locality: Willard Point, Bahia Gonzaga, Baja California Norte, Mexico, 29°48' N, 114°23' W, two to three fathoms in sand.

Etymology: I take great pleasure in naming this species for James H. McLean, great authority on the living mollusks of the northeastern Pacific, who brought this species to my attention.

Remarks: *Macron mcleani* is most similar to *M. lividus*. Both species have a distinctly fibrous periostracum, a broadly fusiform shape, obsolete spiral sculpture, and an appressed suture. *Macron mcleani* differs from *M. lividus* by having a distinct rather than an obsolete labral tooth, by having nine strong lirae instead of nine to twelve very faint lirae on the inner side of the outer lip, and by having a much narrower aperture (apertural height-to-width ratio 3.1 as compared to 2.3 to 2.5 in *M. lividus*). Other relatively smooth species of *Macron* (*M. orcutti* and the early Miocene species being described by Gibson-Smith et al., 1997) have a relatively broader

aperture and a larger number of lirae (thirteen to seventeen) than *M. mcleani*.

Genus *Triumphis* Gray, 1857

Type species: *Buccinum distortum* Wood, 1828, by monotypy.

Diagnosis: Shell large, maximum height 63 mm, ovate; protoconch paucispiral, consisting of 2.25 to 2.5 smooth whorls; spire relatively high, last whorl comprising 66 to 75% of total shell height; spire whorls flattened, sutures appressed; last whorl rounded above in young stages, but with a strong, ridge-like shoulder during final growth stages; basally not constricted; spiral sculpture consisting of two or three cords on spire whorls, one or two low, rounded, below shoulder on last whorl, and five stronger basal cords on last whorl; axial sculpture confined to spire whorls, consisting of ten rounded ribs per whorl; pseudolivid groove and labral spine absent; outer lip more or less planar, its base sharply crenulated at terminations of grooves between basal cords; posterior notch weak, often obsolete in mature shells; inner side of outer lip with ten to eleven long lirae; aperture ovate to elongate-ovate, its height-to-breadth ratio 2.1 to 2.8; posterior end of aperture constricted by massive, rounded parietal ridge; columella with three or four superficial ridges on upper part, and with weak fold at entrance of siphonal canal; columellar and parietal callus often thick, but of very limited extent; siphonal fasciole low, rounded; anterior siphonal notch deep; umbilicus absent.

Stratigraphic and geographic distribution: Early Miocene, southern California; Recent, tropical eastern Pacific.

Discussion: All previous authors who have concerned themselves with the classification of *Triumphis* have assigned it to the Buccinidae. When introducing *Triumphis,* Gray (1857:15) referred his new genus to the Pisaniana (= Pisaniinae), a group which, along with other buccinid subfamilies, he assigned to a greatly expanded Muricidae. Fischer (1884) treated it as a subgenus of *Cominella* Gray, 1850. Cossmann (1901) affirmed this assignment by referring the genus to the subfamily Cominellinae (= Photinae). Thiele (1929) and Wenz (1938–44), however, considered *Triumphis* a subgenus or section of *Cantharus* Röding, 1798, a genus usually assigned to the subfamily Pisaniinae (see Cernohorsky, 1971, 1975). Keen (1971) recognized it as a full genus, but she did not specify where in the family it belongs.

Assignment of *Triumphis* to the Photinae is precluded on three grounds. A heavy periostracum of the kind seen in *Triumphis* is not known in any member of the Photinae, in which the periostracum is either absent or very thin. The outer lip of *Triumphis* has two characteristics inconsistent with assignment of the genus to Photinae. In *Triumphis,* the edge of the outer lip is sharp, and the smooth surface of the inner side of the outer lip does not cross the edge to the outer side. In most Photinae, by contrast, the edge of the outer lip is polished, because the inner layer minutely extends across the edge to the outer side. The anterior part of the outer lip above the siphonal notch lacks a sinus in *Triumphis.* Instead, this part of the lip is planar and bears very strong crenulations. In most Photinae, the outer lip is medially convex, and there is a variably developed concave sinus between the convex sector above and the anterior siphonal notch below. This sinus is so prominent in some genera that it is occasionally referred to as a stromboid notch to emphasize the superficial resemblance with the anterior part of the outer lip in the Strombidae. The sinus in the Photinae is not strongly serrated as is the basal sector of the outer lip in *Triumphis. Triumphis* superficially resembles some members of the Pisaniinae, including *Cantharus* and related genera, in possessing a thick, persistent periostracum, and by having an unreflected, sharp-edged outer lip; but it differs in characters of shell sculpture and in the profile of the outer lip. In *Triumphis,* the strength of spiral sculpture increases from the shoulder to the base. This condition is typical of the Pseudolividae as well as of many other neogastropod groups including the buccinid subfamilies Photinae and Siphonaliinae, and the families Nassariidae, Fasciolariidae, Costellariidae, and clades within the Toxoglossa, among others. This condition contrasts with the situation in the Pisaniinae as well as in most Muricidae, in which spiral sculptural elements increase in prominence from the base to the whorl shoulder. The outer lip of immature and most mature *Triumphis* is characterized by a notch at the junction with the penultimate whorl. Such a notch is absent in Pisaniinae. In the latter subfamily, the outer lip has a convex profile in its medial sector, and a broad, shallow sinus on its upper half. The outer lip of *Triumphis* is strongly crenulated at its edge only along its lower half, as in most other Pseudolividae, whereas in the Pisaniinae it is crenulated along its entire length.

I assign *Triumphis* to the Pseudolividae because of the following combination of characters: persistent periostracum, planar sharp-edged outer lip without anterior sinus, presence of posterior notch, spiral sculpture strongest near base, and outer lip crenulated at ends of basal spiral grooves. *Triumphis* clearly diverges from most other pseudolivids by the absence of a pseudolivid groove and corresponding labral tooth. The point along the edge of the outer lip at which crenulations begin, however, corresponds to the position of the pseudolivid groove and labral tooth in such genera as *Macron* and *Testallium.* Thiele's (1929) description of the rather generalized radula of *Triumphis* is also consistent with placement of *Triumphis* in the Pseudolividae. Anatomical data and molecular sequences will be needed to confirm the phylogenetic affinities of *Triumphis.*

Addicott (1970) referred a single, poorly preserved specimen from the Middle Miocene Olcese Sand of southern California to the genus *Triumphis.* If additional material confirms this assignment, *Triumphis* would have

a record dating back to the middle Miocene. The only other species, *T. distorta*, is known only from the Recent tropical eastern Pacific, where it ranges from El Salvador to northern Peru.

Kilburn and Tankard (1975) described *Triumphis dilemma* from early Pliocene strata in Cape Province, South Africa (see also Kensley and Pether, 1986). Elsewhere (Vermeij, 1997), I have shown that this species is not closely related to *Triumphis*, and I proposed a new genus for it in the buccinid subfamily Photinae.

TAXA EXCLUDED FROM PSEUDOLIVIDAE

Several genera and species included by previous authors in the Pseudolividae or Pseudolivinae or in taxa here assigned to that family do not belong in this group. Some of these are treated below. A few western North American Paleogene species assigned to *Pseudoliva* by previous authors were already excluded by Squires (1989) and will not be discussed further here.

Material examined is listed in Appendix 2. I provide diagnoses for *Melapium*, *Nicema*, and *Seymourosphaera*, because important shell characters of these genera have not been noted previously. My conclusions about the genus *Austrosphaera* are surmised from Oleinik and Zinsmeister's (1996) paper. The Cretaceous genera *Fulgerca*, *Hydrotribulus*, and *Ptychosyca* were so well described by Sohl (1964a, b) that diagnoses for them are superfluous. The important shell attributes of these genera are mentioned below in the discussions of these taxa.

Genus *Nicema* Woodring, 1964

Type species: *Nicema amara* Woodring, 1964, by original designation.

Diagnosis: Shell moderately large, maximum height 57 mm, broadly fusiform; protoconch paucispiral; spire consisting of five to seven teleoconch whorls; spire moderately high, last whorl comprising 68 to 82% of total shell height; sutures appressed, increasingly deep in later growth stages; last whorl rounded or weakly shouldered above, the shoulder a raised ridge in mature specimens of some species; last whorl basally constricted; spiral sculpture consisting of about seven weak cords on spire whorls, and of up to seven cords on and just above basal constriction of last whorl; axial sculpture consisting of eight to ten rounded folds on spire whorls, obsolete or absent on last one or two whorls; pseudolivid groove and labral tooth absent; outer lip medially convex downward, with adapical concave sinus and weak posterior notch; lower sector of outer lip crenulated by ends of grooves between basal cords; upper concave sector of outer lip with smooth edge; inner side of outer lip briefly lirate in adult; aperture elongate-ovate, its height-to-breadth ratio 2.8 to 2.9; inner lip smooth, adherent or very slightly erect; columellar callus very limited in extent; columella smooth, concave, with basal fold at entrance of siphonal canal; parietal rib present; siphonal fasciole prominent, sculptured with spiral threads and bounded adapically by keel; siphonal canal dorsally recurved, with deep anterior notch; umbilicus absent or represented by very narrow slit.

Stratigraphic and geographic distribution: Late Miocene to Recent, tropical eastern Pacific; Late Miocene, Atlantic Panama.

Discussion: Woodring (1964) proposed the genus *Nicema* for several late Miocene buccinids from tropical America. Besides the type species, *N. amara* from the Gatun Formation of Panama, he included *N. guttifera* (Grzybowski, 1899) from northern Peru and *N. predistorta* (Marks, 1951) from the Daule beds of Ecuador. Olsson (1964) considered *Nicema* as a subgenus of *Northia* Gray, 1847, and added his new species *N. noctua* and *N. venada* from the Miocene of Ecuador. Keen (1971) included *Nicema* as a subgenus of *Triumphis*, and added still another species, *N. subrostrata* (Wood, 1828) from the tropical eastern Pacific. Finally, Addicott (1970) tentatively referred *Macron hartmanni* Hertlein & Jordan, 1927, to *Nicema*. I have retained the latter species in *Macron*. All authors except Olsson (1964) considered *Nicema* to be closely related to *Triumphis*.

Despite its morphological similarity to *Triumphis*, *Nicema* may belong to the buccinid subfamily Photinae rather than to the Pseudolividae. *Nicema* resembles *Triumphis* in having a low spire (last whorl comprising 79 to 82% of total shell height in *N. subrostrata*, 68% in *N. noctua*, 73% in *T. distorta*), axial sculpture confined to the spire whorls, an adapical notch, strong rounded parietal rib, adherent smooth inner lip, lirate outer lip, and a persistent periostracum. The most conspicuous differences reside in the spiral sculpture and the shape of the outer lip. In *Nicema*, the constricted basal part of the last whorl is adorned with fine threads, and stronger cords occur above this sector. In *Triumphis*, the strongest sculpture (of five cords) occurs on the unconstricted base. The outer lip of *Triumphis* is essentially planar in profile, whereas that of *Nicema* is medially convex and adapically characterized by a broad, concave, smooth-edged sinus below a shallow notch where the outer lip joins the penultimate whorl.

Characters of the outer lip and the external shell sculpture support Olsson's (1964) suggestion that *Nicema* is related to *Northia* and other genera in the buccinid subfamily Photinae. The only characteristic inconsistent with this assignment is the absence of a sinus on the lower half of the outer lip. Such a sinus characterizes most photines, but not *Nicema*. Anatomical observations on the living *N. subrostrata* will be needed to confirm my assignment of *Nicema* to the Photinae.

In addition to the species assigned to *Nicema* by Woodring (1964), Olsson (1964), and Keen (1971), the genus *Nicema* includes *Clavella solida* Nelson, 1870, from the Late Miocene of northern Peru (see also Vermeij & DeVries, 1997). This species, which Olsson (1932) assigned to the muricid subgenus *Acanthiza* (*Chorus*), has eight to ten strong axial ribs on the spire

whorls, a weakly constricted base, strong fasciolar ridge, and narrow umbilical chink, has the shoulder raised into a ridge in the adult stage. Olsson (1932) perceived a pseudolivid groove, and compared his specimens of *N. solida* to *Gastridium* (= *Testallium*) *cepa* and *Acanthiza (Chorus) voluta* Olsson, 1932, a species here assigned to *Testallium*. My examination of the holotype of *Clavella solida* failed to reveal a pseudolivid groove, and Nelson (1870) did not mention such a feature in his accurate original description of the species. Instead, the last whorl shows an abrupt abapical narrowing near its base. This abrupt narrowing is not like the deeply concave basal constriction of *Nicema subrostrata*, in part because the siphonal canal of *Clavella solida* is not dorsally recurved as it is in other species of *Nicema*, but in other respects Nelson's species resembles members of *Nicema*.

Jung (1995) named the genus *Judaphos* for *J. imparabilis* Jung, 1995, a Late Miocene species from the Pacific coast of Costa Rica. *Judaphos* closely resembles *Nicema* but differs from the latter genus by being more slender and having a less prominent siphonal fasciole. It is possible that *Judaphos* forms a link between *Northia* and *Nicema*.

Genus *Melapium* H. & A. Adams, 1853

Type species: *Pirula lineata* Lamarck, 1822, subsequent designation by Cossmann, 1901.

Diagnosis: Shell large, maximum height 100 mm, globose; protoconch large, paucispiral; spire very low, last whorl comprising 97% or more of total shell height; last whorl evenly rounded above, strongly constricted basally; spiral sculpture consisting of about six low cords on basal constriction; axial sculpture consisting of distinct growth lines; pseudolivid groove and labral tooth absent; outer lip simple, gently and evenly convex; inner side of outer lip smooth; posterior notch weak but present; aperture ovate, its height-to-breadth ratio 2.1; columella with strong fold at entrance of siphonal canal; inner lip adherent; adapical end of inner lip with strong parietal tooth; siphonal fasciole well developed, bounded adapically by prominent keel; siphonal canal dorsally strongly recurved; anterior siphonal notch deep; umbilicus absent; parietal and columellar callus well developed, rendering apertural side of last whorl flattened, but callus not extending onto spire.

Stratigraphic and geographic distribution: Early Pliocene to Recent, southern Africa.

Discussion: The genus *Melapium* was placed in the Strepturidae by Cossmann (1901) and in the Olividae (Pseudolivinae) by Thiele (1929), Wenz (1938–44), and Kilburn (1989). A study of shell and anatomical characters persuaded Kantor (1991) to place *Melapium* in its own family Melapiidae. According to Kantor (1991), *Melapium* differs from Pseudolividae by the absence of accessory salivary glands and of the operculum, and by having the opening of the radular diverticulum to the buccal cavity at the tip rather than at the base of the proboscis. The accessory esophageal gland of *Melapium* is hypertrophied.

The shell of *Melapium* also differs from that of the Pseudolividae. The pseudolivid groove and labral tooth are absent in *Melapium*, and the base of the columella is marked by a prominent fold at the entrance of the siphonal canal. The siphonal canal, moreover, is long and strongly recurved dorsally.

Given the characters of the shell of *Melapium*, I tentatively agree with Cossmann (1901) in assigning the genus to the Strepturidae. *Melapium* differs from the type genus *Strepsidura* Swainson, 1840, by the absence of axial sculpture, and by the presence of a strong parietal tooth. A considerable stratigraphic gap exists between the last appearance of *Strepsidura* in the Late Eocene and the first Pliocene appearance of *Melapium*. Considering the poor pre-Pliocene fossil record in South Africa, such a stratigraphic hiatus does not constitute strong evidence against a phylogenetic link between the Paleogene Strepturidae and the Late Neogene *Melapium*. If *Melapium* does prove to belong to the Strepturidae, the name Melapiidae Kantor, 1991, would fall as a subjective junior synonym of Strepturidae Cossmann, 1901.

The genus *Melapium* is represented by two living species, *M. lineatum* from the temperate coast of South Africa, and *M. elatum* (Schubert & Wagner, 1829) from Natal and Mozambique. Kensley and Pether (1986) additionally recognize two fossil species, *M. patersonae* Bullen Newton, 1913, from the Neogene of Bredasdorp; and *M. hawthornei* Kensley & Pether, 1986, from the 30 m and 50m levels (Early to Middle Pliocene) at Hondeklip Bay, Cape Province, South Africa.

Genus *Austrosphaera* Camacho *in* Furque & Camacho, 1949

Type species: *Austrosphaera glabra* Camacho *in* Furque & Camacho, 1949.

Discussion: Oleinik and Zinsmeister (1996) have given a brief account of this Late Cretaceous and earliest Paleocene genus from Patagonia and Tierra del Fuego, Argentina. The shell is thick, low-spired, and semi-ovate, with short, shallow anterior and posterior canals and a poorly developed siphonal fasciole. Although spiral sculpture, a pseudolivid groove, and a labral tooth are absent, Oleinik and Zinsmeister (1996) assigned *Austrosphaera* with doubt to the buccinid subfamily Pseudolivinae. I have not examined any material of *Austrosphaera*, but on the basis of great similarity with *Seymourosphaera* (see below), I tentatively exclude *Austrosphaera* from the Pseudolividae. Just where this genus should be assigned remains unclear.

Genus *Seymourosphaera* Oleinik & Zinsmeister, 1996

Type species: *Seymourosphaera bulloides* Oleinik & Zinsmeister, 1996, by original designation.

Diagnosis: Shell of medium size, maximum height 41 mm, broadly fusiform; protoconch large, paucispiral, smooth; teleoconch consisting of four to five whorls separated by impressed suture; spire low, last whorl comprising 79 to 94% of total shell height; last whorl evenly rounded on upper part, weakly constricted at base; spiral sculpture consisting of very weak, low, fine cords, best expressed on spire whorls and on upper part of last whorl, but often absent on last whorl and not expressed on base; axial sculpture absent; pseudolivid groove and labral tooth absent; outer lip of mature shell abaxially expanded, weakly convex, slightly thickened and smooth on inner side; posterior notch weak but present; aperture broadly ovate, its height-to-breadth ratio 1.9 to 2.3, adapically narrowed, but outer lip not adapically extended; columella rounded, its profile sigmoid, smooth, without basal fold; parietal callus ventrally thick, extending partly onto spire in some species; inner lip adherent; parietal rib absent; siphonal fasciole absent or low and rounded; anterior siphonal notch very shallow; umbilicus absent.

Stratigraphic and geographic distribution: Early Paleocene, Seymour Island, Antarctic Peninsula.

Discussion: The above diagnosis is based on my examination of paratypes of *S. bulloides* and all the other three members of the genus, very kindly sent to me by Anton Oleinik. When they proposed the genus *Seymourosphaera*, Oleinik and Zinsmeister tentatively assigned it to the buccinid subfamily Pseudolivinae, although they noted that a pseudolivid groove and labral tooth are absent. Two characters are inconsistent with assignment of *Seymourosphaera* to the Pseudolividae. Spiral sculpture is best developed on the upper part of the whorl, and therefore does not increase in prominence abapically as it does in the Pseudolividae. The outer lip of *Seymourosphaera* is abaxially expanded and is somewhat thickened on its smooth inner side; it therefore indicates determinate growth. Pseudolivids never show abaxial expansion of the adult outer lip and apparently continue to grow in the spiral direction throughout life.

Just how *Seymourosphaera* should be classified remains unclear. Despite superficial resemblance to *Melapium*, *Seymourosphaera* is unlikely to belong to the Strepturidae. Members of that family have spiral sculpture increasing in prominence abapically, have a strong basal columellar fold, and display indeterminate growth. *Seymourosphaera* may belong to a large Paleogene complex of buccinoid gastropods with low-spired shells that have no Neogene or Recent relatives.

Oleinik and Zinsmeister (1996) named four species of *Seymourosphaera*, all from a restricted interval of the Early Paleocene Sobral Formation and the uppermost part of the underlying Lopez de Bertodano Formation of Seymour Island, Antarctic Peninsula. All the species are extremely similar to each other, varying only in spire height and in the degree of persistence of the very weak spiral sculpture on the last whorl. I strongly suspect that the three species confined to the Sobral Formation (*S. depressa*, *S. subglobosa*, and *S. bulloides*) are a single species, which would then be known as *S. bulloides*. The fourth and oldest species (*S. elevata*), known from the uppermost Lopez de Bertodano Formation as well as from the Sobral Formation, differs from the others by having a higher spire of five instead of four whorls. It may be a distinct species.

Genus *Fulgerca* Stephenson, 1941

Type species: *Fulgerca venusta* Stephenson, 1941 (=? *Pseudoliva? attenuata* Wade, 1926; see Sohl, 1964b), by original designation.

Discussion: Three genera from the Late Cretaceous of the Atlantic and Gulf Coastal Plain of the United States have often been included in the Pseudolividae, probably because they possess a labral tooth (see Sohl, 1964a, b). One of these is the Santonian to Maastrichtian genus *Fulgerca*. The labral tooth is formed at the end of a fasciolar band at the tapering, unconstricted base of the gently rounded last whorl. The spire is high, the last whorl comprising 50% or more of the total shell height. Sculpture consists of fine spiral and axial elements. Sohl (1964a, b) gives a thorough overview of the group.

Exclusion of *Fulgerca* from the Pseudolividae is supported by several characters, including the high spire and the formation of the labral tooth at the termination of a fasciolar band instead of at the end of a groove above the fasciole. Where *Fulgerca* should be assigned remains unresolved. Ponder (1973) suggested an affinity with the Colubrariidae (now often considered part of the buccinid subfamily Pisaniinae; see Beu & Maxwell, 1987), perhaps because of the elongate fusiform shape, high spire, and finely cancellate sculpture of *Fulgerca*. The labral tooth formed at the end of the fasciolar band would, however, be unique among Pisaniinae. For the present, I prefer to keep the familial assignment of *Fulgerca* open.

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APPENDIX 1

Genera and species of Pseudolividae, together with a list of material examined for this study. The genus in which the species was described is given in parentheses if it differs from the genus to which it is assigned here.

Benthobia Dall, 1889

B. tryonii Dall 1889, type of genus: = *Nux alabaster* Barnard, 1960; *Lacuna cossmanni* Locard, 1897 (see Bouchet & Warén, 1985). **Distribution:** Recent, bathyal and abyssal western and eastern Atlantic, southwestern Indian Ocean, southwestern Pacific. **Material examined:** MNHN (Azores, Gulf of Mexico); USNM 717352 (Tulear, Madagascar), 824174 and 832910 (off Virginia).

Fulmentum Fischer, 1884

F. ancilla (Hanley, 1859) (*Pseudoliva*), type of *Sylvanocochlis* Melvill, 1903. **Distribution:** Recent, Agulhas Bank, South Africa.
F. sepimentum (Rang, 1832) (*Buccinum*), type of *Fulmentum*. **Distribution:** Recent, West Africa (Togo to Angola). **Material examined:** MNHN (Cotonou, Pointe Noire, Cap Esterias, Luanda); CAS 063185 (West Africa).

Fusopsis Ravn, 1939

F. canalifera (Ravn, 1939) (*Pseudoliva*), type of genus. **Distribution:** Paleocene, Copenhagen, Denmark.

Fusulculus Bouchet & Vermeij, 1997

F. albus Bouchet & Vermeij, 1997. **Distribution:** Recent, bathyal, New Caledonia and north of New Zealand. **Material examined:** MNHN.
F. crenatus Bouchet & Vermeij, 1997, type of genus. **Distribution:** Recent, bathyal, Coral Sea to northeast of Fiji. **Material examined:** MNHN (New Caledonia).

Hubachia Etayo Serna, 1979

H. ramirolobae Etayo Serna, 1979, type of genus. Distribution: Paleocene, Guajira, Colombia. **Material examined:** UCMP 16014, 16105.

Luizia Douvillé, 1933

L. costae (Douvillé, 1933) (*Buccinum*), type of genus; = *L. costae* var. *brevis* (Douvillé, 1933). Distribution: Early? Miocene, Angola.
L. zebrina (A. Adams, 1855) (*Pseudoliva*). **Distribution:** Recent, Angola. **Material examined:** MNHN (Luanda, Moçamedes).

Macron H. & A. Adams, 1853

M. aethiops (Reeve, 1847) (*Buccinum*), = *Pseudoliva kellettii* A. Adams, 1855 (type of genus), *Purpura trochlea* Gray, 1839, *auct. non Buccinum trochlea* Bruguière, 1789;
? *Macron wrightii* H. Adams, 1865, ? *M. stereoglypta* Sowerby, 1882 (see Melvill, 1903). **Distribution:** middle Miocene (Olcese Sand), California; Pleistocene to Recent, Pacific coast of Baja California and Isla Danzante, Gulf of California (see Grant & Gale, 1931; Addicott, 1970; Mulliner, 1996). **Material examined:** GJV (Guerrero Negro); Mulliner collection (Isla Danzante); USNM 55665 (Cedros Island), 60074 (San Quentin Island), 60075 (San Quentin Bay), 102256 (Ballena Bay), 105428 (Scammons Lagoon), 105429 (Abreojos), 105432 (San Ignacio), 105433 (Manuel Lagoon), 105434 (Point Abreojos), 253114 (Lagoon Heads), 265240 (Cedros Island), 265601 (San Benito Island), 265613 and 265771 (Point Abreojos), 332389 (Magdalena Bay), 852828 (San Ignacio Lagoon), 1499926 (Gulf of California).
M. constrictus Gibson-Smith, Gibson-Smith & Vermeij, 1997. **Distribution:** early Miocene (Burdigalian, Cantaure Formation), Venezuela. **Material examined:** NMB.
M. hartmanni Hertlein & Jordan, 1927. **Distribution:** middle to late Miocene (San Ignacio Formation), Baja California Sur, Mexico. **Material examined:** CAS 61714.07.
M. lividus (A. Adams, 1855) (*Pseudoliva*), type of *Macroniscus* Thiele, 1929. **Distribution:** Pleistocene to Recent, southern California. **Material examined:** GJV (La Jolla).
M. mcleani Vermeij, 1997. **Distribution:** Recent, Gulf of California. **Material examined:** LACM 2812.
M. merriami Arnold, 1907. **Distribution:** middle Miocene (Temblor Formation), California. **Material examined:** USNM 164982.
?*M. nipponensis* Chinzei, 1959. **Distribution:** Pliocene (Kubo Formation), Honshu, Japan.
M. orcutti Dall, 1918. **Distribution:** Pacific coast, Baja California Sur, Mexico. **Material examined:** LACM 79–26.27 (Punta Marquez), 71–3.26 (Punta Abreojos).

Naudoliva Kilburn, 1989

N. caitlinae Kilburn, 1989, type of genus. **Distribution:** Recent, Transkei, South Africa. **Material Examined:** NM E5750/T107.
N. guppyi (Mansfield, 1925) (*Pseudoliva*). **Distribution:** Late Miocene (Springvale Formation), Trinidad. **Material examined:** USNM 352664.
N. vorsteri Lussi, 1995. **Distribution:** Algoa Bay, South Africa. **Material examined:** ANSP 399956.

Pseudoliva Swainson, 1840

P. crassa (Gmelin, 1791) (*Buccinum*), type of *Pseudoliva*; = *P. striatula* A. Adams, 1854 (see Melvill, 1903). **Distribution:** Recent, southern Angola. **Material examined:** MNHN (Baia dos Tigres, Ilha de Luanda); CAS 063184 (West Africa).
P. lutulenta Kensley & Pether, 1986. **Distribution:** early Pliocene (50-meter level), Hondeklip, Cape Province, South Africa. =? *P. crassa* (see text under *Pseudoliva*).

P. orbignyana Mayer, 1864. **Distribution:** Early? Miocene, Madeira.

Sulcobuccinum d'Orbigny, 1850

S. aaronsohni (Blanckenhorn, 1927) (*Pseudoliva*). **Distribution:** Late Cretaceous (Senonian), Palestine.

S. adelekei (Adegoke, 1977) (*Pseudoliva*). **Distribution:** Paleocene (Ewekoro Formation), Nigeria. **Material examined:** USNM 174853.

S. ambiguum (Binkhorst, 1861) (*Pyrula*). **Distribution:** Late Cretaceous (Maastrichtian), Netherlands and ? Tunisia (see Pervinquière, 1912).

S. bellecomptum (Muniz, 1993) (*Pseudoliva*). **Distribution:** Late Cretaceous (Campanian) (Gramame Formation), northeastern Brazil.

S. bocaserpentis (Maury, 1912) (*Pseudoliva*). **Distribution:** Paleocene (Soldado Formation), Trinidad.

S. breve (Doncieux, 1908) (*Pseudoliva*). *Distribution:* Late Paleocene (Thanetian: Sparnacian), southern France.

S. briarti (Vincent, 1928) (*Pseudoliva*). **Distribution:** Early Paleocene (Danian: Calcaire de Mons), Belgium (see Glibert, 1973). **Material examined:** IRSNB 5467 (Mons) and unnumbered specimen (Ludanovka).

S. bussoni (Albanesi *in* Albanesi & Busson, 1974) (*Pseudoliva*). **Distribution:** Early Eocene (Series 6b), southern Tunisia.

S. carinatum (Conrad, 1860) (*Pseudoliva*). **Distribution:** Middle Eocene (Laredo, Stone City, Cook Mountain Formations, Archusa Marl), Gulf Coastal Plain (see Palmer & Brann, 1966; Dockery, 1980). **Material examined:** ANSP 7032.

S. chavani (Tessier, 1952) (*Pseudoliva*). **Distribution:** Paleocene (Marigot de Balling), Senegal.

S. coniforme (Oppenheim, 1904) (*Pseudoliva*). **Distribution:** Eocene, Cameroon.

S. coronaria (Olsson, 1930) (*Pseudoliva*). **Distribution:** Middle to Late Eocene (Saman and Talara Formations of Olsson, 1930), Peru. **Material examined:** PRI 24221.

S. cretaceum (Kase, 1990) (*Calorebama*). **Distribution:** Late Cretaceous (Late Campanian to Early Maastrichtian: Izumi Group), Japan.

S. curvicostatum (Briart & Cornet, 1870) (*Pseudoliva*). **Distribution:** Early Paleocene (Danian: Calcaire de Mons), Belgium (see Glibert, 1973). **Material examined:** IRSNB 5469, 5470.

S. dechordatum (White, 1887) (*Harpa*). **Distribution:** Paleocene (Maria Farinha Formation), Brazil, ? Early Paleocene (Marigot de Balling), Senegal (see Tessier, 1952). ? = *S. scalina* (see Palmer & Brann, 1966).

S. elegans (Hislop, 1860) (*Pseudoliva*). **Distribution:** Early Paleocene (Danian: Intertrapine beds), Nagpur, India. **Material examined:** BMNH GS10297, 10298, 10299.

S. elisae (Briart & Cornet, 1870) (*Pseudoliva*), = *P. ludovicae, P. grossecostata*, and *P. elongata*, all of Briart & Cornet, 1870 (see Glibert, 1973). **Distribution:** Early Paleocene (Danian: Calcaire de Mons), Belgium. **Material examined:** IRSNB 5471–5474.

S. eschi (Oppenheim, 1904) (*Pseudoliva*). **Distribution:** Eocene, Cameroon; ? Middle Eocene (Ameki Formation), Nigeria.

S. fischeri (Mayer-Eymar, 1887) (*Pseudoliva*). **Distribution:** Late Eocene (Bartonian), Thun, Switzerland.

S. fissuratum (Deshayes, 1835) (*Buccinum*), type of *Sulcobuccinum*. **Distribution:** Late Paleocene (Thanetian), Paris Basin, France. **Material examined:** MNHN (Chenay); RGM 58771 (Chenay).

S. funkeanum funkeanum (Adegoke, 1977) (*Pseudoliva*). **Distribution:** Paleocene (Ewekoro Formation), Nigeria.

S. f. ornatum (Adegoke, 1977) (*Pseudoliva*). **Distribution:** Paleocene (Ewekoro Formation), Nigeria.

S. guineense (Adegoke, 1977) (*Pseudoliva*). **Distribution:** Paleocene (Ewekoro Formation), Nigeria. **Material examined:** USNM 174854, 174855.

S. howardi (Dickerson, 1914) (*Molopophorus*), type of *Pegocomptus* Zinsmeister, 1983; = *Pseudoliva reticulata* Waring, 1915 (see Zinsmeister, 1983). **Distribution:** Late Paleocene (Santa Susana and Sepultura Formations), southern California and Baja California. **Material examined:** LACM IP 22330, 22376, and 22688 (Santa Susana Formation, Simi Hills).

S. iminense (Moret, 1938) (*Pseudoliva*). **Distribution:** Paleocene, Sud-Atlas, Morocco (see Salvan, 1954).

S. japonicum (Nagao, 1924) (*Orthaulax*). **Distribution:** Late Eocene to Early Oligocene (Takashiman, Okinoshiman, Funazuan, and Mazean faunas), Kyushu, Japan (see Honda, 1991, 1994). **Material examined:** IGPS 8068, 8106, 35661 (Futago-Jima), 8069, 35660, 35684, 37769 (Hashima), 8105 (Shiratake), 35743 (Komenoyama), 36176 (Okinoshima), 36186 (Funazu), 36714 (Kiuragi).

S. kitsoni (Newton, 1922) (*Pseudoliva*). **Distribution:** Late Eocene (Ameki Formation), Nigeria (Eames, 1957). **Material examined:** BMNH G42069, 42062, 42070 to 42076.

S. koeneni (Ravn, 1939) (*Pseudoliva*), non *Purpura pusilla* Beyrich, 1854 (see Ravn, 1939). **Distribution:** Paleocene, Copenhagen, Denmark.

S. laudunense (Defrance, 1826) (*Buccinum*), = *Buccinum semicostatum* Deshayes, 1835. **Distribution:** Late Paleocene (Thanetian), Paris Basin, France (see Cossmann, 1889). **Material examined:** UCMP loc. B-5393 (Sinceny; MNHN (Pourcy).

S. leutweini (Böhm, 1926) (*Pseudoliva*). **Distribution:** Eocene, Namibia.

S. libycum (Quaas, 1902) (*Pseudoliva*). **Distribution:** Late Cretaceous (Maastrichtian), Egypt; Early Paleocene (Danian), East Tripoli, Libya.

S. lineatum (Gabb, 1864) (*Pseudoliva*), = *P. dilleri* Dickerson, 1914 (type of *Calorebama* Squires, 1989), *Pseudoliva inornata* Dickerson, 1915, *P. kirbyi* Clark, 1938, *P. markleyensis* Clark, 1938, *P. tejonensis* Dickerson, 1915, *P. volutaeformis* Gabb, 1864 (see text under *Sulcobuccinum*; for different treatment see Squires, 1989). **Distribution:** Early to Late Eocene ("Meganos" to "Tejon" stages), Pacific North America. **Material examined:** UCMP 3679 (*P. dilleri*), 11053 (*P. inornatum*), 12472 (*P. markleyensis*), 15409 (*P. volutaeformis*), 15796 (*P. lineata*).

S. linosum (Conrad, 1860) (*Pseudoliva*), = *Pseudoliva moerens* de Gregorio, 1890 (see Palmer & Brann, 1966). **Distribution:** Middle Eocene (Weches, Stone City, and Cook Mountain Formations), Texas.

S. maritimum (Squires, Zinsmeister & Paredes-Mejia,

1989) (*Popenoeum*), type of *Popenoeum* Squires, Zinsmeister & Paredes-Mejia, 1989; = *Popenoeum maritimus bajacusis* Squires, Zinsmeister & Paredes-Mejia, 1989 (see text under *Sulcobuccinum*). **Distribution:** Paleocene (San Francisquito and Sepultura Formations), Baja California

S. michelini Coquand, 1862, = *Pseudoliva michelini* vars. *longispinata, multispinata,* and *paucispinata,* all of Salvan, 1954. **Distribution:** Middle Eocene (Suessonian), North Africa (see Salvan, 1954).

S. minutissimum (Salvan, 1954) (*Pseudoliva*). **Distribution:** Early Paleocene (Danian: Calcaire de Bouabout), Morocco.

S. moabiticum (Blanckenhorn, 1927) (*Pseudoliva*). **Distribution:** Late Cretaceous (Senonian), Palestine.

S. multinodulosum Vermeij, 1997, = *Pseudoliva chavani* Glibert, 1973, *non* Tessier, 1952 (see text under *Sulcobuccinum*). **Distribution:** Early Paleocene (Danian: Calcaire de Mons), Belgium. **Material examined:** IRSNB 5368.

S. mutabile douvillei (Olsson, 1928) (*Pseudoliva*). **Distribution:** Early Eocene (basal Restin Formation), Peru. Material examined: PRI 3681.

S. m. mutabile (Woods, 1922) (*Pseudoliva*). **Distribution:** Early Eocene (lower Salina Group: Negritos Formation), Peru (see Woods, 1922; Olsson, 1928; Squires *et al.*, 1989).

S. m. woodsi (Olsson, 1928) (*Pseudoliva*). **Distribution:** Early Eocene (upper Salina Group: Negritos Formation), Peru (see Olsson, 1928; Squires *et al.*, 1989). **Material examined:** PRI 3684.

S. nanafaliaense (Aldrich, 1931) (*Pseudoliva*). **Distribution:** Early Eocene (Nanafalia Formation), Alabama.

S. nanum (Gardner, 1945) (*Pseudoliva*). **Distribution:** Paleocene (lower Midway Formation), Nuevo Leon, Mexico.

S. obtusum (Deshayes, 1835) (*Buccinum*), Deshayes, 1865 (see Cossmann, 1889). **Distribution:** Late Paleocene (Thanetian) and Middle Eocene (Lutetian), Paris Basin, France. **Material examined:** MNHN Sapicourt, Boisgeloup).

S. ostrarupis ostrarupis (Harris, 1896) (*Pseudoliva*). **Distribution:** Early Eocene (Bashi Marl Member, Hatchetigbee Formation), Alabama.

S. s. pauper (Harris, 1899) (*Pseudoliva*). **Distribution:** Early Eocene, Texas. **Material examined:** TMM BEG35590 and 35675

S. perspectivum (Conrad, 1860) (*Pseudoliva*). **Distribution:** Late Eocene (Moodys Branch Formation and Yazoo Clay), Mississippi. **Material examined:** GJV; MGS.

S. praecursor (Petbö, 1906) (*Pseudoliva*) **Distribution:** Late Cretaceous (Senonian), Hungary

S. primum (Defrance, 1827) (*Struthiolaria*), = *Buccinum tiara* Deshayes, 1835, *Pseudoliva pursanensis* Doncieux, 1908, *P. binodosa* Traub, 1938 (see Villatte, 1970, Squires *et al.*, 1989). **Distribution:** Late Paleocene (Thanetian), Europe. **Material examined:** IRSNB (Noaille).

S. pusillum (Beyrich, 1854) (*Purpura*), = *Purpura nodulosa* Beyrich, 1854 (see Wrigley, 1941, and text under *Sulcobuccinum*). **Distribution:** Late Eocene (Priabonian: Lattorfian), northwestern Europe.

S. retusum mancorense (Olsson, 1928) (*Pseudoliva*) **Distribution:** Late Eocene (Chira, Mancora, and Heath Formations) and ? Early Oligocene, Peru. **Material examined:** PRI 3679, 3680.

S. r. retusum (Philippi, 1887) (*Gastridium*), = *Pseudoliva parinasensis* Woods, 1922 (Vermeij & DeVries, 1997). **Distribution:** Early Eocene, Algarrobo, Chile; Early to Middle Eocene (Negritos and Talara beds of Olsson, 1928, 1930), Peru; as *Pseudoliva* sp. cf. *P. parinasensis*, Middle Eocene, Colombia (Clark & Durham, 1946). **Material examined:** SGO PI 765; UCMP 5020.

S. r. samanicum (Olsson, 1928) (*Pseudoliva*). **Distribution:** Middle to Late Eocene (Saman and Talara Formations of Olsson, 1928, 1930), Peru (= Verdun Formation), Peru; Late Eocene (Ceru Mainsjie), Curaçao (Jung, 1974). **Material examined:** PRI 3677, 3678; UCMP 35021, 35022 (Colombia).

S. robustum (Briart & Cornet, 1870) (*Pseudoliva*), = *Pseudoliva canaliculata* Briart & Cornet, 1870 (see Glibert, 1973). **Distribution:** Early Paleocene (Danian: Calcaire de Mons), Belgium; ? Early Paleocene, Senegal (Tessier, 1952). **Material examined:** BMNH GS136, S137, IRSNB 5466.

S. rogersi (Adegoke, 1977) (*Pseudoliva*). **Distribution:** Paleocene (Ewekoro Formation), Nigeria.

S. rosenkrantzi (Traub, 1979) (*Pseudoliva*). **Distribution:** Late Paleocene (Oichinger Schichten), Austria.

S. rude (von Koenen, 1889) (*Pseudoliva*). **Distribution:** Late Eocene (Priabonian: Lattorfian), Germany

S. santander (Gardner, 1945) (*Pseudoliva*). **Distribution:** Late Paleocene to Early Eocene (Laredo, Tuscahoma, Wilcox, Hatchetigbee, and Nanafalia Formations), Gulf Coastal Plain of Mexico and the United States (see Dockery, 1980). **Material examined:** MGS (Bells Landing Member, Tuscahoma Formation).

S. scalina (Heilprin, 1881) (*Pseudoliva*). **Distribution:** Early Eocene (Nanafalia and Hatchetigbee Formations), Alabama ? = *dechordata* White, 1887 (see Palmer & Brann, 1966).

S. schweinfurthi (Oppenheim, 1904) (*Pseudoliva*). **Distribution:** Eocene, Cameroon.

S. sofegginense (Rossi Ronchetti, 1959) (*Pseudoliva*). **Distribution:** Late Cretaceous (Maastrichtian), East Tripoli, Libya.

S. subcostatum paucicostatum (Rossi Ronchetti, 1959) (*Pseudoliva*). **Distribution:** Late Cretaceous (Maastrichtian), East Tripoli, Libya.

S. s. subcostatum (Stoliczka, 1867) (*Pseudoliva*). **Distribution:** Early Paleocene (Danian: Arrialoor beds), southern India.

S. tenuicostatum (Briart & Cornet, 1870) (*Pseudoliva*), = *Pseudoliva dubia* Briart & Cornet, 1870 (see Glibert, 1973). **Distribution:** Early Paleocene (Danian: Calcaire de Mons), Belgium. **Material examined:** IRSNB 5475

S. thielei (Böhm, 1926) (*Pseudoliva*). **Distribution:** Eocene, Namibia. ? = *S. kitsoni* (see text under *Sulcobuccinum*).

S. tuberculiferum (Conrad, 1860) (*Pseudoliva*). **Distribution:** Late Paleocene (Gregg's Landing and Bell's Landing Members, Tuscahoma Formation; Nanjemoy Formation) of Gulf and Atlantic coastal Plains

(see Squires, 1989). **Material examined:** MGS, UCMP loc. A-1056 (Bell's Landing Member).

S. unicarinatum (Aldrich, 1886) (*Pseudoliva*). **Distribution:** Early Paleocene (Matthew's Landing Member, Porters Creek Formation), Alabama (Squires, 1989). **Material examined:** MGS.

S. vetustum (Conrad, 1833), type of *Buccinorbis* Conrad, 1865; = *Monoceros fusiformis*, *M. pyruloides*, and *M. sulcatum*, all of Lea, 1833 (see Palmer, 1937). **Distribution:** Middle Eocene (Gosport Sand), Alabama. **Material examined:** GJV (Little Stave Creek), MGS.

S. vientoense (Clark & Durham, 1946) (*Pseudoliva*). **Distribution:** Eocene, Colombia. **Material examined:** UCMP 35023.

S. zittelli (Pethö, 1906) (*Pseudoliva*). **Distribution:** Late Cretaceous (Senonian), Hungary.

S. sp. aff. *S. maritimum* (*Pseudoliva*). **Distribution:** Paleocene (Sonja Member, Agatdal Formation), West Greenland (see Squires *et al.*, 1989; Kollmann & Peel, 1983).

S. sp. (as *Pseudoliva scalina* Heilprin, 1896, *non* Heilprin, 1881). **Distribution:** Early Paleocene (Clayton Member, Porters Creek Formation), Alabama (see Squires *et al.*, 1989).

S. sp. of Olsson, 1934 (*Pseudoliva*). *Distribution:* Late Cretaceous (Maastrichtian: Monte Grande Formation), Peru.

Sulcoliva Vermeij, 1997

S. modesta (Olsson, 1928) (*Pseudoliva*). **Distribution:** Late Eocene (Talara Formation of Olsson, 1930), Peru. **Material examined:** PRI 3668

S. monilis (Olsson, 1928) (*Pseudoliva*), type of genus. **Distribution:** Early Eocene (Parinas Sandstone and Restin Formation), Peru. **Material examined:** PRI 3671.

Testallium Vermeij & DeVries, 1997

T. cepa (Sowerby, 1846) (*Gastridium*), type of genus; = *Monoceros labiale* Hupé, 1854, *Fusus labialis* Hupé, 1854, *Monoceros opimum* Hupé, 1854, *Fusus opimus* Hupé, 1854, *Chorus sp.* aff. *C. blainvillei* of Watters & Fleming, 1972 (see Vermeij & DeVries, 1997). **Distribution:** Early Miocene (Navidad Formation and Punta Ahuenco beds), Chile; Early to Early Middle Miocene (Chilcatay and Pisco Formations), Peru. **Material examined:** BMNH G26399.

T. escalonia Vermeij & DeVries, 1997. **Distribution:** Late Pliocene (La Cueva Formation), Chile. **Material examined:** CAS 66800.01-.02; UCMP 39880.

T. voluta (Olsson, 1932) (*Acanthiza*). **Distribution:** Early Miocene (Heath Formation), Peru (see Vermeij & DeVries, 1997). **Material examined:** PRI 2302.

Triumphis Gray, 1857

T. distorta (Wood, 1828) (*Buccinum*), type of genus; = *Columbella triumphalis* Duclos, 1843 (Keen, 1971). **Distribution:** Recent, tropical eastern Pacific. **Material examined:** GJV (Costa Rica, Panama); USNM 368541 (Payta, Peru).

T. sp. of Addicott, 1970. **Distribution:** Middle Miocene (lower Olcese Sand), California.

Zemira H. & A. Adams, 1853

Z. australis antecursoria Ponder & Darragh, 1975. **Distribution:** Early Miocene (Longfordian and Batesfordian), Victoria, Australia.

Z. a. australis (G. B. Sowerby I, 1833) (*Eburna*), type of *Zemira*; *Zemira praecursoria* Tate, 1888, *Eburnopsis aulacoessa* Tate, 1889 (Ponder & Darragh, 1975). **Distribution:** middle Miocene (Balcombian) to Recent, temperate Australia. **Material examined:** CAS 28597 (Victoria); USNM 130901 (Tanner, Chamberlain), 202777 and 203906 (Westernport).

Z. bodalla Garrard, 1966. **Distribution:** Recent, southern Queensland.

Z. tessellata Tate, 1893. **Distribution:** Jan Juc Formation (Late Oligocene), Victoria. **Material examined:** IRSNB (Spring Hill).

Z. sp. of Ponder & Darragh, 1975. **Distribution:** Glen Aire Clay (Late Eocene), Nigeria. **Material examined:** RGM (Bende).

APPENDIX 2

Material examined of some species belonging to neogastropod families other than Pseudolividae.

Family Olividae, subfamily Ancillinae

Baryspira australis (Sowerby, 1830): GJV (Leigh, New Zealand)

Eburna glabrata (Linnaeus, 1758): GJV (near Punto Fijo, Venezuela)

Family Strepturidae

Melapium lineatum (Lamarck, 1822): USNM 687845 and 609711 (Jeffreys Bay, South Africa)

Strepsidura turgida (Solander *in* Brander, 1766): UCMP Localities B-5357 (Cressay, Late Eocene), B-5404 (Fleury-la-Rivière, Middle Eocene), B-5402 (Herouval, Late Eocene), B-6484 (Levignen, Late Eocene), all Paris Basin, France.

Family Buccinidae, subfamily Photinae

Cominella acutinodosa (Reeve, 1846): USNM 691693 and 691707 (Bandicoot Bay, Barrow Island, Western Australia)

Iosepha glandiformis (Reeve, 1847): GJV (several localities near Leigh and Dunedin, New Zealand)

I. tasmanica Tenison-Woods, 1878: USNM 638596 (Dunsborough, Western Australia)

Nicema amara Woodring, 1964: USNM 243665 (lower Gatun Formation, Panama)

N. noctua (Olsson, 1964): USNM 644018 and 645271 (Angostura Formation, Ecuador, Late Miocene)

N. solida (Nelson, 1870): YPM 00507 (Cardalitos beds, Peru, Late Miocene; see Vermeij & DeVries, 1997)

N. subrostrata (Wood, 1828): GJV (San Blas, Mexico)

N. venada (Olsson, 1964): USNM 644019 (Rio Cayapas, Ecuador; Late Miocene)

Family Melongenidae, subfamily Echinofulgurinae

Cornulina minax (Solander *in* Brander, 1766): MNHN (Late Eocene, Paris Basin); UCMP Locality B-5356 (Crenes, France; Middle Eocene).

Protobusycon cretaceum (Wade, 1917): USNM 32897 (Coon Creek, Tennessee; Late Cretaceous: Maastrichtian)

Families uncertain

Hydrotribulus elegans Sohl, 1964: MGS (Coon Creek, Tennessee; Late Cretaceous: Maastrichtian) *nodosus* Wade, 1916: USNM 32915 and 130456 (Coon Creek, Tennessee; Late Cretaceous: Maastrichtian)

Laccinum lugardi (Newton, 1922): RGM (Ameki Formation, Late Eocene, Nigeria)

Lacinia alveata (Conrad, 1833): GJV, UCMP Loc. A-959 (Gosport Sand, Middle Eocene, Alabama)

Ptychosyca inornata (Gabb, 1876): USNM 13454 and 13455 (Ripley Formation, Late Cretaceous (Maastrichtian) of Tippah County, Mississippi)

Seymourosphaera bulloides Oleinik & Zinsmeister, 1996: PU Localities 1136, 1430, 1501 (*S. bulloides*); 9 (*S. depressa*); 1434 and 1435 (*S. subglobosa*); 1328 and 1138 (*S. elevata*) (all names of Oleinik & Zinsmeister, 1996), all Paleocene of Seymour Island, Antarctica.

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Recent Genera and Species of the Family Haliotidae Rafinesque, 1815 (Gastropoda: Vetigastropoda)

D. L. Geiger
Department of Biological Sciences
University of Southern California
Los Angeles, CA 90089–0371USA
dgeiger@scf. usc. edu

ABSTRACT

A new assessment of all the Recent taxa of the family Haliotidae is presented. The 17 Recent and one fossil genus-level taxa are evaluated based on their type species. These taxa are recommended not to be used until a comprehensive phylogenetic analysis of the family is available. The approximately 200 nominate, species-level taxa in the Hahotidae are reviewed. Fifty-five species with ten additional subspecies are considered valid. The following new synonymies are proposed: *Haliotis brazieri* Angas, 1869, + *melculus* (Iredale, 1927); *H. hargravesi* Cox, 1869, + *ethologus* (Iredale, 1927); *H. jacnensis* Reeve, 1846, + *hanleyi* Ancey, 1881; *H. marmorata* Linnaeus, 1758, + *guineensis* Gmelin, 1791, + *rosacea* Reeve, 1846; *H. pustulata* Reeve, 1846, + *jousseaumi* Mabille, 1888; *H. rubiginosa* Reeve, 1846, + *howensis* (Iredale, 1929); *H. rugosa* Lamarck, 1822, + *multiperforata* Reeve, 1846, + *revelata* Deshayes, 1863; *H. striata* Linnaeus, 1758, + *lamellosa* Lamarck, 1822; *H. tuberculata* Linnaeus, 1758, + *incisa* Reeve, 1846, + *japonica* Reeve, 1846, + *reticulata* Reeve, 1846; *H. varia* Linnaeus, 1758, + *barbouri* Foster, 1945, + *dringii* Reeve, 1846, + *gemma* Reeve, 1846. *Haliotis neglecta* Philippi, 1848, is resurrected as a valid species from the Mediterranean Lectotypes for *H. multiperforata* Reeve, 1846, and *H. revelata* Deshayes, 1863, are selected For all taxa considered valid the geographic distribution and sources of published illustrations are given. Infrequently illustrated species are figured.

Key words: Gastropoda. Haliotidae, taxonomy, synonymies, lectotypes, zoogeography.

INTRODUCTION

Members of the family Haliotidae (abalone) occur in most tropical and temperate oceans, particularly in the shallow subtidal zone. The first mention of abalone in the literature was made in the fourth century B.C. by Aristotle. In the first century A.D. the name of *otia* (little ear) was used by Pliny. In Japan, abalone were mentioned as early as the fourth century A.D. In the medieval literature of Europe they were noted for the first time by Gessner in 1553. The first good illustrations were provided by Buonanni, Lister, Gualtieri, and Rumphius between 1681 and 1741; these were later cited by Linnaeus (1758). The pre-Linnean descriptions of abalone have been dealt with more extensively in Crofts (1929), Cox (1962) and Muller (1984a).

Taxonomic publications on the family began with Linnaeus (1758), who described the first seven species of abalone using his system of binominal nomenclature. His work was continued and enlarged by Gmelin (1791), who added 12 taxa. Reeve (1846) described 43 new taxa in his monograph, which is one of the most important sources for the taxonomy of the family Haliotidae. In the late nineteenth century, three larger monographs were published by Sowerby (1882), Weinkauff (1883), and Pilsbry (1890), but only a few new taxa were introduced by these authors. Wagner and Abbott (1978) provided a list of taxa including tentative synonymies. Kaicher (1981) illustrated all the species and subspecies she considered valid, providing the most comprehensive means available to identify the Recent Haliotidae. Pickery (1991) listed most abalone taxa chronologically, including their references. Ubaldi (1993) has started to publish a series intended to cover, in alphabetical order, all extant haliotid species; to date, four species have been treated by Ubaldi.

The latest valid species described is *Haliotis roberti* McLean, 1970. *Haliotis coccinea canariensis* Nordsieck, 1975, is the most recent taxon that has been described. All taxa have been based on shells; only the neotype of *H. unilateralis* Lamarck, 1822, and the types of a new species from Brazil are complete specimens with the animal (Geiger, 1996; Simone, in press).

The alpha taxonomy of the majority of species has been uncertain, except for most of the important commercial species. Between 30 (Dauphin *et al.*, 1989) and 130 (Cox, 1962) of the more than 200 species-level taxa described have been considered valid species. Most authors have estimated the number of distinct species to be approximately 75 (Thiele, 1931; Pickery, 1980; Kaicher, 1981; Lindberg, 1992). The objective here is to reevaluate this family, to critically review all the published information, and to include additional unpublished observations. This groundwork is necessary in the light of a forthcoming phylogenetic analysis of the entire family, because the working unit—the species—should be clear-

ly understood so that the data matrix will not be obscured by unresolved taxonomic problems.

The conclusions that form the substance of this paper are presented in three lists: Index, Notes, and Valid Species by Faunal Regions. The alphabetical index and the valid species by faunal regions are both cross-referenced to the notes. Species illustrated are those that are infrequently shown in other publications.

MATERIALS AND METHODS

This work is based on a number of visits to major museums in Europe and the United States, where the available type specimens were examined. Museum material was supplemented with specimens from private collections, including those of Katharine Stewart (Carmel, California), Don Pisor (La Jolla, California), Roger Pickery (Wilrijk, Belgium), Mark Jones (Auckland, New Zealand), and Benjamin Singer (Rehovot, Israel). Every original description was carefully checked in the original language. An effort was made to track all relevant secondary literature through later citations and the *Zoological Record*. Some results from ongoing studies of the animals are mentioned where they help in the understanding of taxonomic questions; a detailed coverage of the characters of the animals is beyond the scope of the present contribution and will be provided elsewhere. The radular terminology of Geiger (1996) is used.

The statistical analysis of the shell morphometrical data was performed with STATISTICA™ Mac 4.1 (StatSoft, 1994). For the breakpoint regression, piecewise linear regression with Quasi-Newton estimation method and least-square loss function was employed. Linear regression on the data sets on either side of the breakpoint yielded the slope statistics.

Abbreviations used are: ANSP: Academy of Natural Sciences, Philadelphia; BMNH: The Natural History Museum, London; DMNH: Delaware Museum of Natural History, Wilmington, Delaware; HUJ: Hebrew University, Jerusalem; KBIN: Koniglich Belgische Institut for Natuurwetenschappen, Brussels; LACM: Los Angeles County Museum of Natural History; LSL: Linnean Society London; MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MNHN: Muséum national d'Histoire naturelle, Paris; MHNG: Muséum d'Histoire Naturelle, Genève; NMW: National Museum Wales, Cardiff; SAM: South Australian Museum, Adelaide; SBMNH: Santa Barbara Museum of Natural History, California; USNM: National Museum of Natural History, Smithsonian Institution, Washington.

SYSTEMATIC AFFINITIES AND CHARACTERISTICS OF THE FAMILY HALIOTIDAE

Haliotidae are part of the prosobranch Vetigastropoda, having the nacreous shell, certain characters in the cleavage pattern, a streptoneurous nervous system, two bipectinate ctenidia (gills) served by two heart atria (Diotocardia), and possessing ctenidial bursicles (Hickman, 1988; Haszprunar, 1987; 1993 for review). The row of tremata in abalone and the slit of the pleurotomariids (Pleurotomariidae) are homologous structures, but are not diagnostic characters (Delhaes, 1909; Haszprunar, 1993).

Historically, the Haliotidae were considered to be closely related to the Pleurotomariidae and the Scissurellidae and were united with these families in the superfamily Pleurotomarioidea. The rhipidoglossan radula was thought to be a common character for the Pleurotomariidae and the Haliotidae. However, the radula in the two families differs in many ways. The rows of the radular teeth are almost symmetrical in Haliotidae, but in the Pleurotomariidae they are distinctly asymmetrical. The rachidian tooth is well-formed in the Haliotidae, but reduced in the Pleurotomariidae. The fine outer marginal teeth in the Haliotidae show denticulate cusps (Wu and Huang: 1989; Herbert, 1990; Geiger, 1996; Stewart and Geiger, in press). In the Pleurotomariidae, however, a fan of articulated bristles is found (Hickman, 1984; Harasewych and Askew, 1993; Anseeuw and Goto, 1996). A comparison of the Pleurotomariidae and the Haliotidae to the Scissurellidae is not appropriate, because the latter are subjected to different evolutionary constraints due to their small size and their detrital diet (Fretter and Graham, 1976; Herbert, 1986), which is reflected in their radular structure. The radulae of juvenile abalone were examined by Tong (1985), and are similar to those of small Trochidae (Hickman and McLean, 1990), and Scissurellidae (Marshall, 1993). The independence of radular morphology from feeding ecology has to be questioned due to the extensive morphological plasticity of the radula in response to the feeding ecology of the respective animals. The radulae of the Pleurotomariidae and the Haliotidae will not help to resolve their phylogenetic relationship, because the former is that of a specialized spongivore, the latter that of a strict macroalgal herbivore. The coding of paedo- and peramorphic structures adds further problems, as in the case of the radular characters of the Scissurellidae and the Haliotidae. Either stage-specific structures are considered, which overstate the degree of differentiation. The rachidian in mature animals is serrate in Scissurellidae, but bears a smooth cutting edge in the Haliotidae. Alternatively, heterochronic processes are taken into account, creating characters with inapplicable character states. In this case the serrate rachidian tooth of animals <5 mm unites the Scissurellidae and Haliotidae, but the rachidian characters for animals > 10 mm are inapplicable to the Scissurellidae. The use of the radula to resolve family level relationships within the Vetigastropoda is, therefore, questionable (see also Haszprunar, 1993).

The nearly symmetrical body plan of *Haliotis* has been cited as being plesiomorphic, which situates the group very close to the root of the flexoglossate prosobranchs (Fleure, 1904; Salvini-Plawen and Haszprunar, 1987). This view is supported by the primitive sperm ultrastruc-

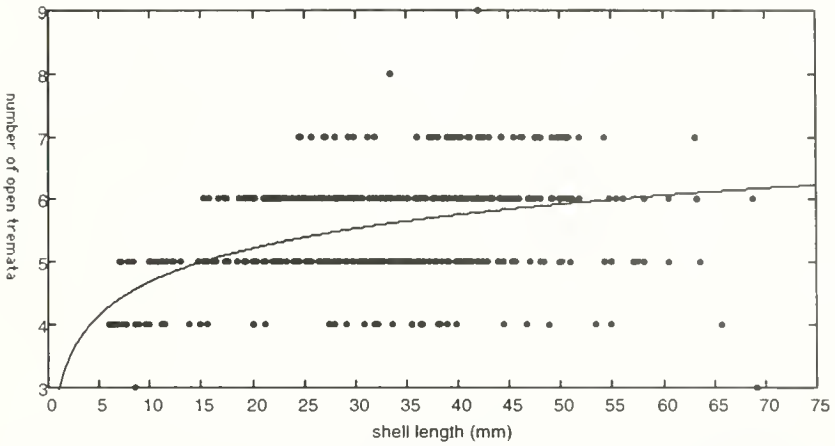


Figure 1. Plot of shell length versus number of open tremata in *H. tuberculata* from numerous Mediterranean populations (n = 433). Note the positive correlation between the two parameters, for which a logarithmic curve has been fitted. Note the intersection with the x-axis around 2 mm shell length, the size at which the first perforation is formed. The first specimens with five open tremata are found at 7 mm, those with six open tremata at 15 mm, those with seven open tremata at 24 mm.

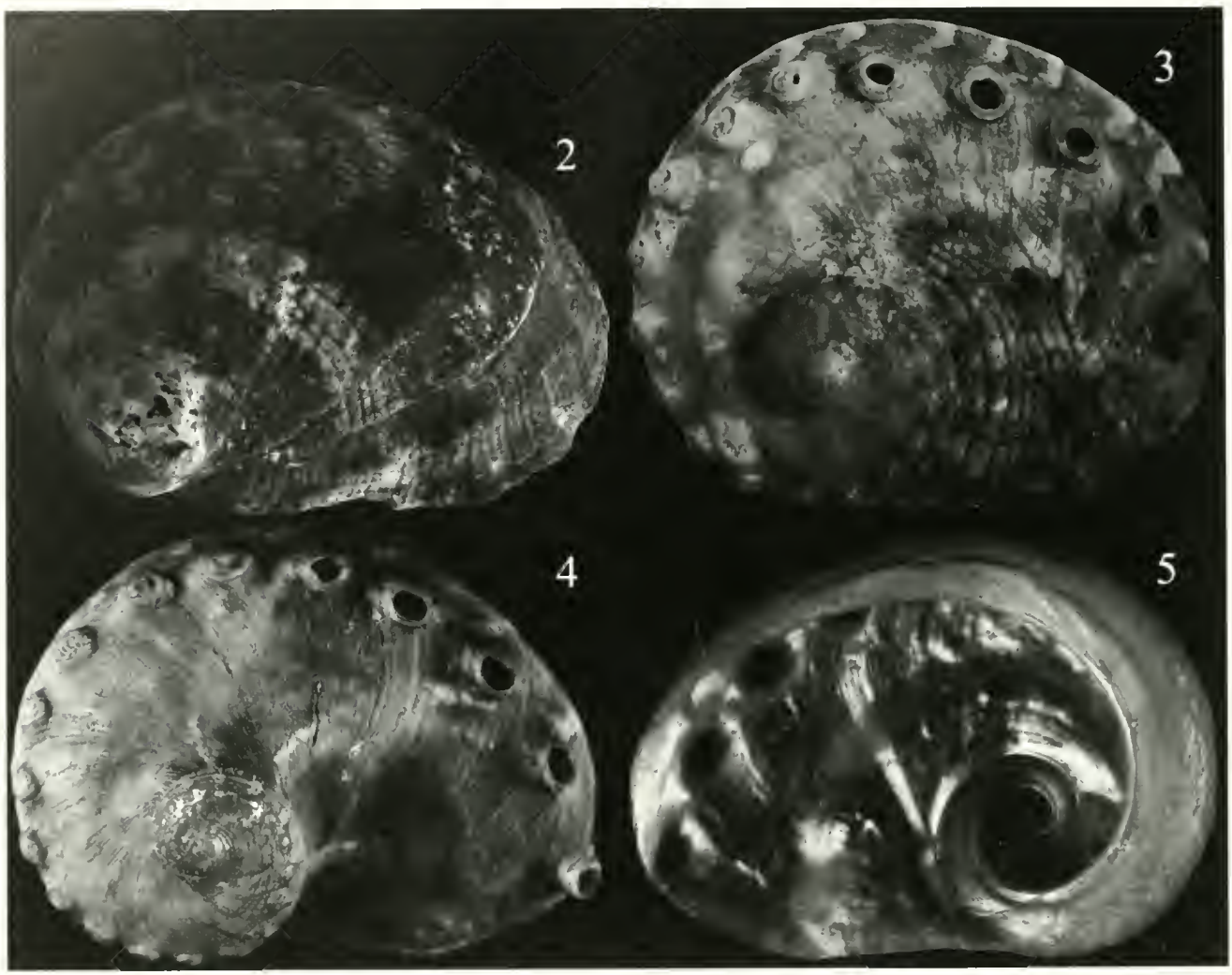
ture (Lewis *et al.*, 1980; Healy, 1988; 1990; Healy and Harasewych, 1992). However, several left parts of the paired body structures, *e.g.*, the gonad and the kidney, are reduced or modified in Haliotidae (Crofts, 1929; Haszprunar, 1988a). The nervous system is close to the primitive condition of *Pleurotomaria*, but in Haliotidae the additional structures of the epipodium and the osphradium are innervated by pleural and visceral elements, respectively. The Haliotidae and the Trochidae have synapomorphic osphradial characters (Haszprunar, 1985; 1993), but the Trochidae are clearly separated from the Scissurellidae, Pleurotomariidae and Haliotidae by the lack of the right ctenidium and associated organs (Salvini-Plawen and Haszprunar, 1987).

The three families within the former superfamily Pleurotomarioidea are now placed in their nominal superfamilies, *i.e.*, the Haliotidae are now in the Haliotioidea, on the same level as the Pleurotomarioidea, Scissurelloidea and the remaining Vetigastropoda (Haszprunar, 1988b; Healy and Harasewych, 1992).

PROBLEMS PERTAINING TO THE TAXONOMY OF THE FAMILY HALIOTIDAE

Tremata as a taxonomic character and teratological type specimens: Members of the family Haliotidae can be easily recognized by the depressed shell and the tremata, the row of holes used for respiration, release of gametes, and defecation (Ino, 1952; Tissot, 1992; Voltzow and Collin, 1995). One may potentially confuse them with some members of the Stomatellinae, a trochid subfamily (Hickman and McLean, 1990; Pickery, 1995). Some taxa with imperforate shells described in the genus *Haliotis* are actually Stomatellinae (*e.g.*, *H. impertusa* Burrow, 1815), and are not dealt with here. Stomatellids that resemble haliotids (*Gena, Stomatella* and *Microtis*) are rather small (< 40 mm), have no right ctenidium, a flat shell, no tremata, and no spiral sculpture. They might suggest imperforate specimens of juvenile *H. asinina* Linnaeus, 1758, but the latter have several distinct spiral ridges (see Kaicher, 1981), which are no longer formed as the shell grows larger than 3.5 to 4 cm. Specimens of the trochid genus *Granata* have been erroneously identified as imperforate *H. cyclobates* Péron, 1816 (Geiger, pers. obs.).

In most descriptions of abalone the number of open tremata is indicated, erroneously suggesting that the number is diagnostic for identification at the species level. However, the number of open tremata changes during the growth of the shell (Hemphill, 1907; Sinclair, 1963). The larval shell has no tremata at all; the first one is formed at a size of approximately 1–3 mm (Crofts, 1929; Murayama, 1935; Bonnot 1940; Ino, 1952; Shibui, 1971; Mu *et al.*, 1976; Bevelander, 1987). Figure 1 shows the size dependent change of the number of open holes for the European *H. tuberculata* Linnaeus, 1758. Linear breakpoint regression (r^2=0.69) estimated the breakpoint at 5.5 open holes, corresponding to a size of approximately 33 mm, where the slope changes from 3.8 (SE = 0.53) to 0.0017 (SE = 0.56). The number of open tremata varies greatly within a species and between populations (Hemphill, 1907; Schepman, 1909; Sinclair, 1963; Talmadge, 1960; Geiger and Groves, submitted). Therefore, the notion that the number of open tremata or total number of tremata is fixed within any given species is misleading. Taxa erected solely because of differences in the number of open tremata have to be rejected, as in the case of *H. multiperforata* Reeve, 1846 (note 32), or *H. cracherodii* Leach, 1814, with its subspecies *bonita* Orcutt, 1900, and *californiensis* Swainson, 1822. Specimens from some populations on Guadalupe Island off Baja California show the morphology of *H. cracherodii californiensis*. These specimens have more and smaller tremata, which are also more closely spaced than in specimens from the mainland. Specimens from populations having the *californiensis* morphology that have



Figures 2–5. Infrequently illustrated *Haliotis*. **2.** *Haliotis* cf. *diversicolor* Reeve, 1846. 28 mm. MNHN [not numbered]. No locality data. An imperforate specimen of *Haliotis*. **3.** *H. brazieri—hargravesi*. 31 mm. K. A. Stewart collection. Solitary Island, Coffs Harbour, New South Wales, Australia. This specimen begins growth with the smooth morphology of *H. brazieri*, but midway changes to the spiral ridges typical of *H. hargravesi*. **4–5.** *H. brazieri* Angas, 1869. 29 mm. MHNG [not numbered]. Australia.

been cultured on the mainland of central California changed the size and spacing of the tremata to those of typical *H. cracherodii cracherodii* (B. Owen, pers. comm.); this indicates that these characters are under environmental control.

Imperforate abalone shells have been found (Smith, 1893; Marquand, 1906; Hemphill, 1907; Dall, 1919; Leighton, 1960; Geiger, pers. obs.; Figure 2), but are rather rare. Even rarer are specimens with a double row of tremata (Smith, 1888; Hamada, 1982). A somewhat larger number of specimens with a continuous slit instead of the row of tremata are known (*H. laevigata*: Gray, 1856; *H. asinina*, *H. cracherodii*, *H. parva* Linnaeus, 1758, *H. planata* Sowerby, 1882, *H. rufescens* Swainson, 1822, *H. tuberculata*: Geiger, pers. obs.). New tremata are formed at the anterior margin of the shell, and posteriorly the mantle eventually seals them when they are no longer functional. Occasionally one to several tremata are closed out of the sequence just described (Geiger, 1991: fig. 8; *H. parva*, *H. pulcherrima* Gmelin, 1791: Geiger, pers. obs.). Only in *H. elegans* Philippi, 1844, is this phenomenon found regularly and becomes the rule in large specimens (see Wilson, 1993: pl. 3, figs. 2A, 2B).

Haliotis imperforata Dall, 1919, *H. lusus* Finlay, 1927, and *H. holzneri* Hemphill, 1907, are based on imperforate type specimens. It is clear that these are teratological shells not warranting taxonomic recognition (note 66).

Three type specimens show further deformities. *Haliotis sieboldii* Reeve, 1846, (note 64) has been described from a distorted shell, where the row of tremata is located much closer to the periphery of the shell. The same applies also to *H. whitehousei* (Colman, 1959) (note 55), although the distortion is not as pronounced as in *H. sieboldii*. This type of a deformation is also

known from some specimens of *H. cracherodii* (LACM 23452; SBMNH 13522; USNM 199890). *Haliotis diegoensis* Orcutt, 1900, (note 65) has an extremely thick and stout shell, a growth form that had been induced by boring organisms, most likely sabellid polychaetes.

Hybrids: The occurrence of hybrids may be challenging to the biological species concept, but can be better understood from the standpoint of the evolutionary species concept. As long as the two species that hybridize keep their identity, they remain intact; otherwise reticulate speciation takes place (*cf.* Wiley, 1981). When discussing hybrids, it is assumed at the outset that the two parent specimens belong to two discrete species, which may not be the case. We may also have a case of unrealized intraspecific variability within a single species.

Hybridization among the Californian species is well determined and studied on the basis of the shell, the epipodium, and by using immunological techniques. Hybrid specimens with intermediate shell and epipodial characters occurred with a frequency of approximately 1:500 (Owen *et al.*, 1971). These authors also found evidence for back crosses of hybrids with some of the parental species, demonstrating that the F1 hybrids are fertile. These results were later corroborated by laboratory rearings (Leighton, 1988). The identity of the recognized species was confirmed with DNA sequence data (Lee and Vacquier, 1992; 1995). Although hybrids involving *H. cracherodii* were successfully reared in the laboratory (Leighton, 1988), these are noticeably absent in the natural environment. This can be accounted for by two factors. First, *H. cracherodii* has an entirely smooth and uniformly black shell, whereas all the other California species show some sculpture and may have a color pattern in the shell. As it is much more difficult to generate a new character (sculpture, color pattern), than to modify an existing one, the simple condition in *H. cracherodii* prevails in hybrid specimens ('overshaddowing effect'). Second, *H. cracherodii* is the only Californian abalone found in the intertidal region. The species is ecologically separated from the remaining species. Within the remaining six Californian species, 13 out of the 15 possible combinations have been documented (Talmadge, 1977b; Leighton, 1988). The two missing hybrids both involve *H. fulgens* Philippi, 1845, which has been shown in the phylogenetic analysis of DNA sequence data to be slightly more distantly related to the other species found in California (Lee and Vacquier, 1995). Prezygotic barriers (analogous to pre-mating barriers in broadcast spawners), such as spawning season and vertical distribution of the species, have to be taken into account. Unfortunately, no information on the fertility of F2 and backcross specimens is available, although many profound changes affecting the fertility may take place after the F1 generation (see King, 1993 for review).

In a second case, two Australian species *H. laevigata* and *H. rubra* Leach, 1914, form hybrids that occur in nature (Anonymous, 1973; R. Fallu, pers. comm.). These two species are also well-known and have been shown to be distinct species (Brown, 1993; Lee and Vacquier, 1995). In this case, hybrids have been identified on the basis of enzyme electrophoresis data. The hybrids occur in varying frequency between 0% and 2% in several populations studied. Good evidence has been presented for the presence of backcrosses of hybrids with either parental species. The hybrids are not believed to represent a starting point of reticulate speciation because of the different habitat requirements of the two species, which is strongly reflected particularly in the thickness of the shell (Shepherd, 1973; Brown, 1995).

Hybrids are reported from two sympatric populations of the two subspecies of *H. discus* Reeve, 1846, *H. discus discus* and *H. discus hannai* Ino, 1952 (Fujino *et al.*, 1980; Sasaki *et al.*, 1980). Although a case of sympatric subspecies may seem a contradiction in terms, it can be seen as a necessary step of gradual, sympatric speciation (see Futuyma, 1986). As the two subspecies are very difficult to distinguish, enzyme electrophoresis was used to identify them with polymorphic loci of several enzymes. Later the same data and method were used to identify hybrids between the two taxa considered. It is not clear whether the variability of one biological species was rather extensive, or whether true hybrids were found; no data on the identification of the specimens studied using alternative methods had been mentioned.

Yet another case is the least clear and has not been discussed in the literature to date. It involves the following taxa from southeastern Australia: *H. brazieri* Angas, 1869, *H. ethologus* (Iredale, 1927), *H. hargravesi* Cox, 1869, and *H. meleulus* (Iredale, 1927), all uncommon to rare. I regard *H. meleulus* as a synonym of *H. brazieri*, and *H. ethologus* a synonym of *H. hargravesi* (notes 62, 66 and 72). *Haliotis hargravesi* shows extensive intraspecific variation in relation to number and elevation of spiral ribs present on the dorsal surface of the shell. *Haliotis brazieri* (Figures 4–5) has no spiral sculpture at all, only an uneven but smooth surface. Intergrading specimens, *i.e.*, potential hybrids, show slight spiral grooves, which, however, are much less distinct than any form within the range of *H. hargravesi*. In some specimens the early whorls lack spiral cords; these will appear abruptly later during shell growth (Figure 3). Such patterns suggest a highly variable species with a few conchological forms. The above observations do not support taxonomic separation of these forms.

M. Jones (pers. comm.) noted that *H. brazieri* and *H. hargravesi* are separated by their vertical distribution. *Haliotis brazieri* occurs from the lower reef surface to 40 m and *H. hargravesi* from 40 m downward to the slope of the reef, where they can be found under coral heads and boulders. Coleman (198:86) confirmed the relatively deep water habitat ("15 to 40 m") of *H. hargravesi*. Hybrids are most often found around 40 m, the depth where the vertical ranges of the two species overlap. Specimens of *H. brazieri* and *H. hargravesi* have been found under the same boulder. The epipodium of

Table 1. Genus-level taxa in the family Haliotidae. od: original designation. m: monotypy. sd: subsequent designation.

Taxon	Valid type species	Original type species (if different)
Euhaliotis Wenz, 1938	*midae* Linnaeus, 1758 [od]	
Eurotis Habe and Kosuge, 1964	*tuberculata* Linnaeus, 1758 [m]	
Exohaliotis Cotton and Godfrey, 1933	*cyclobates* Péron and Lesueur, 1816 [m]	
Haliotis Linnaeus, 1758	*asinina* Linnaeus, 1758 [sd: Montfort, 1810]	
Marinauris Iredale, 1927	*brazieri* Angas, 1869	*meleulus* Iredale, 1927 [sd: Wenz, 1938]
Miohaliotis Itoigawa and Tomida, 1982	*amabilis* Itoigawa and Tomida, 1982 [m]	
Neohaliotis Cotton and Godfrey, 1933	*scalaris* Leach, 1814 [od]	
Nordotis Habe and Kosuge, 1964	*gigantea* Gmelin, 1791 [od]	
Notohaliotis Cotton and Godfrey, 1933	*rubra* Leach, 1814	*naevosa* Martyn, 1784 [od]
Ovinotis Cotton, 1943	*ovina* Gmelin, 1791 [od]	
Padollus Montfort, 1810	*parva* Linnaeus, 1758	*rubicundus* Montfort, 1810 [m]
Paua Fleming, 1952	*iris* Gmelin, 1791 [m]	
Sanhaliotis Iredale, 1929	*varia* Linnaeus, 1758 [od]	
Schismotis Gray, 1856	*laevigata* Donovan, 1808	*excisa* Gray, 1856 [not available]
Sulculus Adams and Adams, 1854	*tuberculata* Linnaeus, 1758	*incisa* Reeve, 1846 [sd: Cossmann, 1918]
Teinotis Adams and Adams, 1854	*asinina* Linnaeus, 1758 [m]	
Tinotis Fischer, 1885	*asinina* Linnaeus, 1758 [obj. syn. of *Haliotis*]	
Usahaliotis Habe and Kosuge, 1964	*cracherodii* Leach, 1814 [m]	

the hybrid specimens showed intermediate characteristics (M. Jones, pers. comm.).

It is well known that abalone show gregarious spawning behavior (Murayama, 1935; Shepherd, 1986). Hybrids may appear under the circumstances described above. Vacquier and co-workers (Vacquier *et al.*, 1990; Lee and Vacquier, 1992; 1995; Vacquier and Lee, 1993; Lee *et al.*, 1995) have demonstrated that although the protein lysin from the head of the acrosomal vesicle in the head of the sperm strongly promotes intraspecific fertilization, it does not fully prevent interspecific fertilization. Although no good data on the frequency of the Australian hybrids are available, it is evidently rather low. It is open to discussion whether we observe here a case of an erratic fertilization pattern of two distinct species, or whether two recently diverged species still occasionally form hybrids, or whether we stand at the cradle of a reticulate speciation event.

GENUS-LEVEL TAXA

A list of all supraspecific taxa of the family Haliotidae is given in Table 1. Comments on a few taxa are given here.

Haliotis, sensu stricto: The subsequently designated type species (Montfort, 1810) of the genus *Haliotis, H. asinina,* has been accepted by the majority of authors (*e.g.*, Iredale, 1910; Kennard *et al.*, 1931; Wenz, 1938; Talmadge, 1963a; Ubaldi, 1985; 1993). Other species have been cited as type species, but those citations are erroneous (*e.g.*, Cossmann, 1918: *H. tuberculata.* Thiele, 1931; Cotton, 1943; Cox, 1962: *H. midae* Linnaeus, 1758. Children *fide* Kennard *et al.*, 1931: *H. iris* Gmelin, 1791). The type designation by Montfort (1810) was unfortunate because he chose as type species the most atypical species within the family. The two presumed type specimens of *H. asinina* are deposited in the LSL, and correspond with what is currently known as this species. The type locality has been designated as Amboina (= Ambon), Indonesia (Talmadge, 1963a). Cotton (1943: 176) discussed the status of *H. asinina* as type species and following Adams and Adams (1853–1858) stated "that *asinina* is the genotype of the *Haliotis* of Montfort 1810 and not of the true *Haliotis* Linnaeus 1758," a statement in contradiction with the original text. Montfort (1810:115) only introduced *Padollus* as a new genus: ". . . nous avons cru pouvoir en former un genre particulier" (. . . we have thought to be able to form from it a distinct genus). *Haliotis asinina* is only designated as type of the genus *Haliotis* on page 120: "Sous la dénomination d'oreille de mer, tous les anciens conchyliologues avoient déjà reconnu ce genre . . . . Nous avons choisi pour type, au lieu de l'haliotide commun (haliotis vulgaris, haliotis tuberculata [*sic*]), celui auquel on a donné le nom d'oreille d'âne" (Under the name of ear of the sea, all the old conchologists have already known this genus. . . . We have chosen as type, instead of the common abalone (*Haliotis vulgaris, Haliotis tuberculata*), the one, for which one has given the name of donkey's ear [*H. asinina*]). Montfort clearly designated the type species of Linnaeus' *Haliotis*, and not a monospecific genus for *H. asinina,* because two other taxa are included under *Haliotis.* The fact that a common name is used in the text of the designation (see ICZN Article 12c) does not invalidate it. Monfort (1810:119) used the following titles for the description of the species: "*Espèce servant de type au genre. Haliotide oreille d'ane. Haliotis asininus.*" (Species serving as type of the genus. Haliotid Donkey's ear. *Haliotis asininus*). First, the type species is clearly designated, and second, the association between common name and scientific name is unequivocal.

The name *Haliotis* stems from the two Greek words *halios* (the sea) and *ous, otis* (the ear). The gender of the genus is feminine because Linnaeus used the femi-

nine ending for the species-level taxa derived from an adjective, particularly for *H. asinina*, the type species of the genus by subsequent designation of Montfort (1810).

Other genus-level taxa, and their type species: One objective synonym (a taxon based on the same type species) of *Haliotis* has been introduced, *H. asinina*: *Teinotis* Adams and Adams, 1854. Note that *The Genera of Recent Mollusca* by Adams and Adams (1853–1858) has as a publication date of 1858 on the inside cover, but in Volume 2 (p. 661) the actual publication dates of the various parts were indicated. For part 14 on Haliotidae the date is June 1854; this latter is the correct date for Adams and Adams' abalone taxa.

The genus *Padollus* Montfort, 1810, with the type species by monotypy, *P. rubicundus* Montfort, 1810 (*non H. rubicunda* Röding, 1798: see note 20), is problematic. *Haliotis scalaris* (Leach, 1814) has been listed as the type species of *Padollus* (*e.g.*, Knight *et al.*, 1960; Wagner and Abbott, 1978; Lindberg, 1992:16), but *P. rubicundus* Montfort is a synonym of *H. parva* and not of *H. scalaris* (see note 20); therefore, the valid type species for *Padollus* is *H. parva*. The fact that the type species in the original description of *Padollus* is no longer invalid does not invalidate the description (ICZN Recommendation 67B). *Haliotis rubicunda* (Montfort) can be unequivocally identified and the senior synonym is the correct, valid type species.

Neohaliotis Cotton and Godfrey, 1933, has been synonymized with *Padollus* on the basis of having the same type species: *H. scalaris* (see above: Pickery, 1991). However, as I have shown that *H. rubicundus* Montfort is not a synonym of *H. scalaris* but of *H. parva*, the synonymy of *Neohaliotis* with *Padollus* has to be rejected.

The type species of *Sulculus* Adams and Adams, 1854, is *H. incisa* Reeve, 1846, which is a synonym of *H. tuberculata* (see also note 16). As *H. tuberculata* has also been chosen as the type species of *Eurotis* Habe and Kosuge, 1964, the latter is now a subjective, junior synonym of *Sulculus*.

Most genus-level taxa had their type species designated by the original author. These designations made in the nineteenth century may not meet modern conventions for designation of a type species in respect to the specificity of the language used. However, I (unlike Fleming, 1952) interpret "explicitly designated" (ICZN Article 67b) somewhat more generously.

Adams and Adams (1853–1858) gave the genus name, followed by its diagnosis and the mention of one particular species as "Ex." (example = type species). This example cannot be confused with the species considered to belong in that genus, which were listed further below in smaller print and in two columns. This form had been utilized for all the genera (*Haliotis* Linnaeus, *Teinotis* H. and A. Adams, *Padollus* Montfort), but not for the subgenus *Sulculus*, where no example was given. I consider this construction as an explicit designation (ICZN Article 67b), which cannot be confused with the exception mentioned under ICZN Article 67c1 ("mention of a species as an example of a genus or subgenus") in conjunction with the example that follows in the Code. The narrow reading of the word "example" shall not obscure the clear intentions of the authors. Fleming (1952) did not accept the designation for *Teinotis* and attributed the subsequent designation to Cossmann (1918).

Marinauris was described by Iredale (1927) without any perceptible intention to designate either *M. meleulus* or *M. ethologus* as the type species; the genus was introduced in an extremely casual form. Fleming (1952: 229) made claims for the designation ("Type (here designated)"), but had overlooked the clear designation by Wenz (1938:172).

Schismotis Gray, 1856, has been given in some lists (Pickery, 1991; Ubaldi, 1993). Gray did not intend to introduce a new name for the specimens he discussed as monstrosities of *H. albicans* Quoy and Gaimard, 1834 (= *H. laevigata*), but only indicated a suitable, hypothetical name. The name is a *nomen nudum* and is not available (see also note 70).

Halcotis Binkhorst, 1861, has been cited as an objective synonym of *Haliotis*, *i.e.*, is treated as an available emendation of *Haliotis* (*e.g.*, Knight *et al.*, 1960). An emendation according to ICZN 33b(i) and 33b(iii) must be "demonstrably intentional," otherwise it is considered as an incorrect subsequent spelling (ICZN 33c), which is not available. As there was no demonstrable intent of the author to emend the original spelling, the name must be considered as unavailable. *Tinotis* Fischer, 1885, however, is available as the author has shown a clear intent to emend the name (Fischer, 1885:845): "*Tinotis* H. et A. Adams, *em.* (*Teinotis*)." It is an objective synonym of *Haliotis*.

Use of genus-level taxa: Some authors (*e.g.*, Talmadge, 1963a; Habe and Kosuge, 1964; Hara and Fujio, 1992) have used several genera in the family Haliotidae. Pickery (1991) provided a list and all references for the Recent taxa, which have been ranked as genera or subgenera (Table 1). As pointed out recently (Geiger, 1996), I consider the usage of these genera to be unjustified at this time for the following reasons:

1) In the descriptions of the one fossil (Itoigawa and Tomida, 1982) and the 17 Recent supraspecific taxa only the type species had been assigned, occasionally with selected species listed. Of the 200 species-level taxa only approximately 83 have ever been assigned to any supraspecific taxon, and 22 of those to more than one group, demonstrating the problematic supraspecific taxonomy of the haliotids. The descriptions of these genus-group taxa are entirely typological and no author has attempted to provide serious differential diagnoses.

2) Only two studies have utilized systematic characters other than shell morphology to determine the relationships of haliotid species. Brown (1993) studied 17 species using enzyme electrophoresis, and Lee and Vacquier (1995) used cDNA sequences of the sperm acrosomal protein lysin (see Vacquier and Lee, 1993 for re-

view) of 22 haliotids. The nominal supraspecific taxa and the limited number of associated species are not in accordance with the groups hypothesized by these more recent studies. However, the type species of *Haliotis*, *H. asinina* (see above for discussion), was not included in either study, making any sound taxonomic decisions impossible.

3) The only inferable consensus in the literature (McLean, 1966:151–153; Lindberg, 1992) as well among abalone researchers (Workshop "Evolutionary Biology and Genetics of Abalone" during the Second International Symposium on Abalone Biology, Fisheries and Culture, February 1994, Hobart, Tasmania) was not to use any genus-level taxa other than *Haliotis*. Yet there was an equally strong consensus among the workshop participants that the diversity within the family may well justify the recognition of several genus-level taxa. However, monophyletic groups will have to be determined from a phylogenetic study encompassing the majority of haliotid species.

SPECIES-LEVEL TAXA

Use of subspecies: Subspecies are defined as allopatric populations with a fixed character (Futuyma, 1986). They do not yet represent discrete, evolutionary lineages. Interbreeding at the periphery of these populations is not necessarily a sign of the erroneous application of the subspecific classification, but will show that the populations are not yet independent species or discrete lineages. Only in very few shallow-water, broadcast-spawning gastropods have subspecies been described, but in *Haliotis* these have been invoked a number of times (Lindberg, 1992), *i.e.*, in the following groups: *H. discus*, *H. mariae* Wood, 1828, *H. pustulata* Reeve, 1846, *H. rubra*, *H. scalaris*, *H. tuberculata*, *H. varia*, *H. virginea* Gmelin, 1791, and the populations of Californian haliotids occurring on Guadalupe Island off Baja California, Mexico. In most cases the subspecific division is found along a temperature gradient; *i.e.*, subspecies are described from different latitudes and not from different longitudes. Most continental coast lines run in a north-south direction, which may be used to explain the above observation. On the other hand, the Indo-Malayan Archipelago offers rich opportunities for the developent of isolated populations, but no subspecies have been proposed for species with a wide longitudinal range such as *H. asinina* (Thailand-Fiji), *H. clathrata* Reeve (East Africa-Samoa), *H. ovina* (Maldives-Tonga), or *H. planata* (Thailand-Fiji). The exceptions to the latitudinal pattern are two southern Australian species, *H. scalaris* and *H. rubra*.

In *H. discus*, the caryotypes differ between the two subspecies (Nakamura, 1985), although their populations interbreed at their common boundary (reviewed in Fujino, 1992). In this case the two taxa are more likely to represent subspecies than ecomorphs.

The two formerly recognized subspecies of *H. tuberculata*—*H. tuberculata tuberculata* and *H. tuberculata lamellosa* Lamarck, 1822—have identical caryotypes (Colombera and Taghiaferri, 1983), and have been recently shown to have identical sequences of the lysin protein (Lee and Vacquier, 1995; see also note 5).

In New Zealand, four geographically separated subspecies of *H. virginea* Gmelin are reported (note 60): *H. virginea virginea*, *H. virginea crispata* Gould, 1847, *H. virginea morioria* Powell, 1938, and *H. virginea huttoni* Filhol, 1880 (Kaicher, 1981; Ubaldi, 1986). These subspecies show gradual changes in several morphological characters used to distinguish them due to environmental parameters associated with geographical location (Talmadge, 1957a). M. Jones (pers. comm.) has found some other forms on the very remote islands off New Zealand that seem to be more stable and distinct than the subspecies mentioned above. In these two cases the described subspecies seem to be ecomorphs not justifying taxonomic separation. However, as no hard data is available for the subspecies of *H. virginea* and, because they are widely used, they are here retained.

None of the Californian subspecies is retained because in those cases for which data is available (*H. cracherodii californiensis*, *H. corrugata diegoensis*: see above and note 65), they have been shown to be mere ecomorphs or teratological specimens. One former species has been allocated at the subspecies rank (*H. kamtschatkana assimilis* Dall, 1878: see McLean, 1966; Owen *et al.*, 1971; note 67).

Two pairs of subspecies are found in southern Australia. These are longitudinally separated: the eastern *H. r. rubra* with the western *H. rubra conicopora* Péron, 1816 (see note 53), and the eastern *H. scalaris emmae* Reeve, 1846, with the western *H. s. scalaris* (see note 56). Information other than shell morphology (Shepherd, 1973; Brown, 1993) suggests one polymorphic species in both instances. However, the shells can be distinguished reasonably well, and the geographic distribution of the morphs is more or less disjunct. The available data suggests subspecific status for the respective populations.

Due to the limited information currently available, the last three cases are provisionally studied as follows: *H. mariae dentata* Jonas, 1846, is easily recognized by the deep furrows resulting in the denticulated anterior margin of the shell, which are missing in the nominate subspecies. The biogeographical data on the species is scant. No assessment of geographic variation is possible. I retain the two subspecies of *H. mariae*.

Haliotis pustulata cruenta Reeve, 1846, has a reddish coloration, a very flat shell, and is found particularly in the Red Sea. *Haliotis pustulata pustulata* on the other hand is more sculptured, usually dark green to mud colored, and is found along the east African mainland. There are no striking differences between the animals, and molecular data on the two morphs is not yet available. I tentatively retain the two subspecies. However, as their relation to *H. rugosa* Lamarck, 1822, is currently unresolved (see note 12), they may eventually be treated as subspecies of *H. rugosa*, or may be united in a single species without further division into subspecies.

Table 2. Differences between the valid taxa of this study with their status in Wagner and Abbott (1978) and illustrations in Kaicher (1981). Subspecies rank is indicated by indentation under the respective species. The following taxa were regarded as valid by Wagner and Abbott (1978) but are here variously synonymized (see Index for details): *canariensis, dringii, gibba, hanleyi, howensis, japonica, kraussi, tuberculata lamellosa, melculus, multiperforata, sulcosa, vixlirata, whitehousei*. Forms listed by Kaicher (1981) have been ignored unless specifically indicated. The following taxa shown by Kaicher (1981) are either variously synonymized here, or she illustrated specimens that cannot be identified (see Index for details): *bistriata, corrugata owenı, dissona, elevata, gemma, multiperforata, scpiculata, whitehousei*.

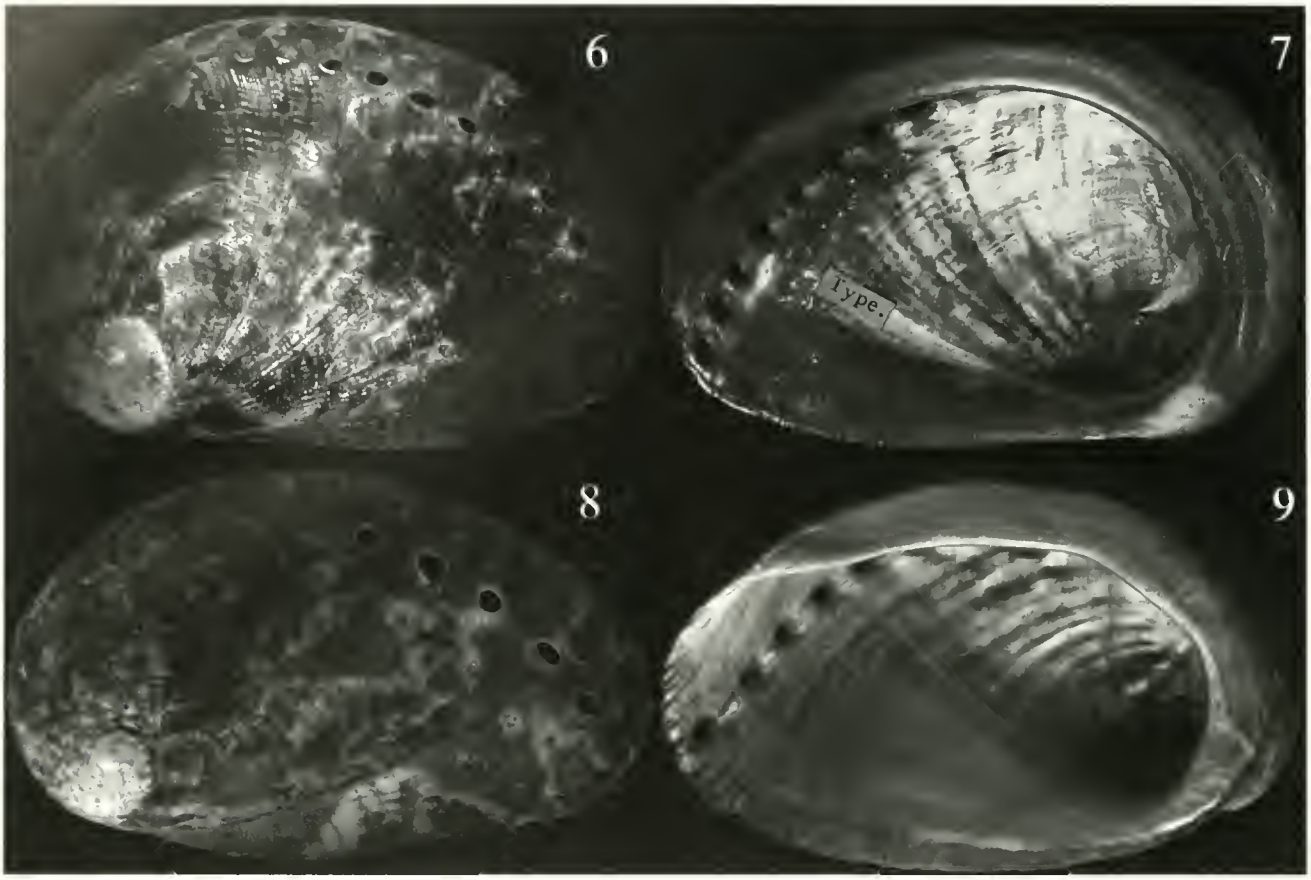
This study	Wagner and Abbott (1978)	Kaicher (1981)
brazieri Angas, 1869	*brazieri*	also as *melculus*
cracherodii Leach, 1814	*cracherodii*	including all ssp.
clathrata Reeve, 1846	as *rubra clathrata*	also as *crebriscalpta* auct. and *venusta*
diversicolor Reeve, 1846	not mentioned	also as *aquatilis* and all ssp.
dohrniana Dunker, 1863	"no information"	*dohrniana*
planata Sowerby, 1882	*planata*	also as *grayana*
hargravesi Cox, 1869	*hargravesi*	also as *ethologus*
jacnensis Reeve, 1846	*jacnensis*	also as *hanleyi*
kamtschatkana Jonas, 1845	*kamtschatkana*	also as *aulaea*
assimilis Dall, 1878	*assimilis*	*assimilis*
mariae dentata Jonas, 1846	not mentioned	*mariae dentata*
madaka (Habe, 1977)	not mentioned	not mentioned
marmorata Linnaeus, 1758	undetermined species	as *guincensis*
neglecta Philippi, 1848	not mentioned	not mentioned
ovina Gmelin, 1791	*ovina*	shows *cyclobates*
pustulata Reeve, 1846	*pustulata*	also as *revelata*
cruenta Reeve, 1846	not mentioned	*cruenta*
roei Gray, 1826	*roei*	also as *sulcosa*
rubiginosa Reeve, 1846	synonym of *varia*	as *varia rubiginosa, howensis*
rubra Leach, 1814	*rubra*	also as *ancile*
conicopora Péron, 1816	*conicopora*	*conicopora*
rugosa Lamarck, 1822	synonym of *tuberculata*	as *pustulata* form *alternata*
scalaris emmae Péron, 1816	*emmae*	*emmae*
speciosa Reeve, 1846	synonym of *fulgens*	*speciosa*
squamosa Gray, 1826	*squamosa*	cf. *diversicolor* shown
tuberculata Linnaeus, 1758	*tuberculata*	also as *lamellosa*
coccinea Reeve, 1846	*coccinea*	also as *zealandica*
unilateralis Lamarck, 1822	*unilateralis*	*varia* shown
varia Linnaeus, 1758	*varia*	also as *unilateralis, dringii* and ssp. *papulata, pustulifera, viridis*
virginea Gmelin, 1791	*virginea*	also as *gibba*
crispata Gould, 1847	as form of *virginea*	*crispata*
huttoni Filhol, 1880	as form of *virginea*	*huttoni*
morioria Powell, 1938	as form of *virginea*	*morioria*

For *H. varia*, seven subspecies are regularly found in the literature, but none are recognized here. As the name suggests, this species is extremely variable. I have been unable to find any geographic pattern, and intermediate specimens abound. These taxa are clear evidence of the typological thinking of the nineteenth century.

Index: In this section I give my opinion of the taxonomic status of every taxon of Recent Haliotidae. Spelling mistakes, erroneous dates, and incorrect taxon-author combinations have not been included, unless widespread confusion exists. Controversial opinions and new assessments of the taxonomic status of various taxa are indicated in the "Notes" that follow. The notes are arranged according to their appearance in the section "Valid Species by Faunal Region" below, *i.e.*, are grouped by valid species.

The two most recent, but brief, taxonomic assessments of the family Haliotidae were provided by Wagner and Abbott (1978) and Kaicher (1981). All differences between the present study and the opinion of these authors are listed in Table 2.

An analysis of all the species-level taxa reveals that only 27% of described taxa are still considered valid species. The status of the subspecies (5%) is very much debated, as the unit of a subspecies is somewhat vaguely defined as a geographically limited population with a certain character, raising the percentage of all valid taxa to slightly less than one-third (see also discussion below). Taxa that had originally been described as either forms or varieties are excluded from modern taxonomy, and represent what we generally call ecomorphs. I do not use Latin form names in an informal fashion (*contra* Reid, 1996), as all available evidence for Haliotidae sug-



Figures 6–9. Infrequently illustrated *Haliotis*. **6–7.** *Haliotis multiperforata* Reeve, 1846. 63 mm. BMNH. Mus. Cuming. Lectotype here selected. **8–9.** *H. revelata* Deshayes, 1863. 58 mm. MNHN. Bourbon. Lectotype here selected.

gests that such taxa do not constitute discrete gene pools. The invalid taxa—synonyms (46%), homonyms (5%), *nomina dubia* (6%), *nomina nuda* (2%), ecomorphs (6%), unavailable names (3%)—account for over two-thirds of all published species-level taxa.

The status of some taxa is still unclear; some may never be fully resolved due the loss of type material, in other cases there is currently too little material available to make a definitive assessment. Unresolved cases are mentioned here. The type of *H. canaliculata* Fischer, 1907, was lost prior to 1872 (Ivanov and Kantor, 1991) and its synonymy with *H. parva* is uncertain (note 19). The following taxa can only be tentatively synonymized, because the type material remains to be located and the original description and/or illustration do not allow a clear assessment: *crenata* Swainson, 1822, *glabra* Swainson, 1822, *scutulum* Reeve, 1846 (notes 47, 48), *sepiculata* Reeve, 1846, and *sinuata* Perry, 1811 (note 22). Seven taxa cannot be identified and are treated as *nomina dubia*: *adriatica* Nardo, 1847, *bistriata* Gmelin, 1791 (notes 5, 14), *imperforata* Gmelin, 1791 (*not* Dall, 1919) (note 66), *interrupta* Valenciennes, 1831 (note 73), *parma* Valenciennes, 1831 (note 73), *plicata* Gmelin, 1791, and *rotundata* Perry, 1811 (note 22). The taxa *maculata* Küster, 1840 (note 18), *maculosa* Küster, 1840 (note 18), *modesta* auct. (note 75), *secernenda* Monterosato, and *schrocteri* Menke (note 76) are treated as *nomina nuda,* because they could not be traced to the original source. The deposited type specimen of *H. victoriae* Brazier is, in the absence of an original description, a *nomen nudum* (note 77). *Haliotis neglecta* Philippi, 1848, is tentatively resurrected but the material available is very limited and restricted to shells only (notes 5, 8, 9). *Haliotis exigua* Dunker, 1863, is tentatively retained as a valid species (note 63).

Lectotypes are here selected for two taxa: *H. multiperforata* Reeve, 1846 (note 32), and *H. revelata* Deshayes, 1863 (note 12). The figured type specimen of unknown provenance of *H. multiperforata*, which is here designated as lectotype (Figures 6–7), is clearly a specimen of *H. rugosa* Lamarck (note 12), however, with rather weak spiral sculpture. The two other specimens in the lot are *H. tuberculata*. The number of open tremata of these specimens is somewhat higher than the usual, but not beyond the expected and documented range of the latter species (data not shown). Consequently a taxonomic separation is not justified.

Haliotis revelata Deshayes, 1863, was described from Île de Bourbon (= Reunion Island). The MNHN holds three lots of type material of this species with a total of

six specimens. One lot with a single specimen is labeled as "ex auteur," another of three specimens is labeled as "syntypes," and a third lot with two specimens is called "type." From the labeling of the specimens, it is not clear which one may be the holotype; therefore, all six specimens are presumed to be syntypes. Deshayes' original illustrations (plate 36, figs. 1 and 2), were meticulously drawn, but cannot be matched to any of the shells in the MNHN. In fact, the illustrations do not resemble any of the species found on Reunion Island, possibly due to excessive artistic freedom. The rather long description lacks much necessary detail. Only two quantitative indications are of some help. The length of the largest specimen (61 mm) and the cited six open perforations are applicable to one specimen in the third lot, but this specimen has irregular growth on the columella that is clearly not illustrated or mentioned. The illustration shows only a weak growth line at the level of the penultimate hole, which is also found in the second specimens of the third lot. This specimen is here designated lectotype (Figures 8–9), the remainder become paralectotypes. *Haliotis revelata* is identified as *H. rugosa* Lamarck, a species common at the type locality. The status of *H. rugosa* Lamarck itself is not resolved (see also note 12).

Haliotis fatui is an unpublished name by the late H. Rehder (USNM) given to specimens that somewhat resemble *H. varia* Linnaeus, 1758. Ubaldi (1993) listed *H. fatui* with the authority "Rheder [*sic*], 1981 ?". This listing is a *nomen nudum* (see also note 71).

In the index that follows, the taxa with their status and/or the currently recognized valid species name are given. The taxa in boldface are currently recognized as valid species and subspecies with the original genus given if different from *Haliotis* s.s. The numbers in brackets refer to the notes that follow. Abbreviations: juv.: juvenile shell; *s.l.*: *sensu lato*; ssp.: subspecies; syn.: synonym; var.: variety, form; ?: uncertain statement (status, identification).

adriatica Nardo, 1847: *nomen dubium*
albicans Quoy and Gaimard, 1834: *laevigata* Donovan, 1808
alfredensis Bartsch, 1915: *speciosa* Reeve, 1846
aliena (Iredale, 1929) [in *Sanhaliotis*]: *varia* var. *papulata* Reeve, 1846
alcata Röding, 1798: *australis* Gmelin, 1791
alternata Sowerby, 1882: *rugosa* Lamarck, 1822 [31]
ancile Reeve, 1846: juv. *rubra* Leach, 1814 [52]
aquatilis Reeve, 1846: *diversicolor* Reeve, 1846
asinina Linnaeus, 1758: valid [4]
asinum Donovan, 1808: *asinina* Linnaeus, 1758
assimilis Dall, 1878: ssp. of *kamtschatkana* Jonas, 1845 [67]
astricta Reeve, 1846: var. of *varia* Linnaeus, 1758
aulaea Bartsch, 1940: *kamtschatkana assimilis* Dall, 1878 [67]
sp. nov. Simone, in press: valid [1]
australis Gmelin, 1791: valid
barbouri Foster, 1946: *varia* Linnaeus, 1758 [1]
bistriata Gmelin, 1791: *nomen dubium*, *tuberculata* Linnaeus, 1758, *s.l.* [5, 14]
bistriata Costa, 1829: homonym, var., syn. of *tuberculata* var. *lamellosa* Lamarck, 1822
bisundata Monterosato: *tuberculata* var. *lamellosa* Lamarck, 1822 [15]
bonita Orcutt, 1900: *cracherodii* var. *californiensis* Swainson, 1822
brazieri Angas, 1869: valid [34, 35]
caelata Röding, 1798: *ovina* Gmelin, 1758
californiana Valenciennes, 1831: *rufescens* Swainson, 1822
californiensis Swainson, 1822: var., syn. of *cracherodii* Leach, 1814
canaliculata Fischer, 1807: *parva* Linnaeus, 1758 ? [19]
canaliculata Lamarck, 1822: homonym, *parva* Linnaeus, 1758
canariensis Nordsieck, 1975: *tuberculata coccinea* Reeve, 1846
capensis Dunker, 1844: *midae* Linnaeus, 1758
carinata Swainson, 1822: *parva* Linnaeus, 1758
cingulata Röding, 1798: *parva* Linnaeus, 1758
clathrata Lichtenstein, 1794: *elegans* Philippi, 1844 [25]
clathrata Reeve, 1846: valid (homonym) [24, 25]
coccinea Reeve, 1846: ssp. of *tuberculata* Linnaeus, 1758 [17, 18]
coccoradiata Reeve, 1846: valid [49]
concinna Reeve, 1846: *varia* Linnaeus, 1758
conicopora Péron, 1816: ssp. of *rubra* Leach, 1814 [53]
corcanica Weinkauff, 1883: *nomen nudum* [68]
corrugata Wood, 1828: valid [26]
costata Swainson, 1822: *australis* Gmelin, 1791
cracherodii Leach, 1814: valid
crebrisculpta Sowerby, 1914: valid [25, 36]
crenata Swainson, 1822: *scalaris* Leach, 1814 ?
crispata Gould, 1847: ssp. of *virginea* Gmelin, 1791 [60]
cruenta Reeve, 1846: ssp. of *pustulata* Reeve, 1846 [10]
cunninghami Gray, 1826: *rubra conicopora* Péron, 1816 [27, 53]
cyclobates Péron, 1816: valid
dalli Henderson, 1915: valid [2]
decussata Philippi, 1850: *marmorata* Linnaeus, 1758 [7]
dentata Jonas, 1846: ssp., var. of *mariae* Wood, 1828
diegoensis Orcutt, 1900: var. of *corrugata* Wood, 1828 [65]
discus Reeve, 1846: valid [62]
dissona (Iredale, 1929) [in *Sanhaliotis*]: valid [36, 39]
diversicolor Reeve, 1846: valid [37]
dohrniana Dunker, 1863: valid [40]
dringii Reeve, 1846: *varia* Linnaeus, 1758 [45]
dubia Lamarck, 1822: *nomen dubium* [69]
echinata Sowerby, 1882: *jacnensis* Reeve, 1846 [31, 41]
elatior Pilsbry, 1890: var. of *midae* Linnaeus, 1758
elegans Philippi, 1844: valid [23, 50]
elevata Sowerby, 1882: *squamata* Reeve, 1846 [31, 57]
emmae Reeve, 1846: ssp. of *scalaris* Leach, 1814 [56]
ethologus (Iredale, 1927): *hargravesi* Cox, 1869 [34]
excavata Lamarck, 1822: *cyclobates* Péron, 1816
excisa Gray, 1856: unavailable, *laevigata* Donovan, 1808 [70]
exigua Dunker, 1877: valid [63]
expansa Talmadge, 1954: *cracherodii* Leach, 1814
fatui Rehder, 1981: unavailable [71]
ficiformis Menke, 1844: *spadicea* Donovan, 1808
fulgens Philippi, 1845: valid
funebris Reeve, 1846: *squamata* Reeve, 1846 [58]
gemma Reeve, 1846: *varia* Linnaeus, 1758 [46]
gibba Philippi, 1846: *virginea* Gmelin, 1791 [61]
gigantea Chemnitz, 1788: unavailable, *gigantea* Gmelin, 1791 [59, 64]
gigantea Gmelin, 1791: valid [64]
gigas Röding, 1798: *gigantea* Gmelin, 1791
glabra Chemnitz, 1788: unavailable, *glabra* Gmelin, 1791 [59]

glabra Gmelin, 1791: valid
glabra Swainson, 1822: homonym, *laevigata* Donovan, 1808 ?
granti Pritchard and Gatliff, 1902: *rubra conicopora* Péron, 1816 [53]
granulata Röding, 1798: *varia* Linnaeus, 1758
grayana Sowerby, 1882: *planata* Sowerby, 1882 [31]
gruneri Philippi, 1848: var., syn. of *diversicolor* Reeve, 1846
guadalupensis Talmadge, 1964: var. of *fulgens* Philippi, 1845
guineensis Gmelin, 1791: *marmorata* Linnaeus, 1758
hanleyana Sowerby, 1882: *nomen dubium* [31, 72]
hanleyi Ancey, 1881: *jacnensis* Reeve, 1846 [41]
hannai Ino, 1953: ssp. of *discus* Gmelin, 1791
hargravesi Cox, 1869: valid [34, 35]
hattorii Bartsch, 1940: var. of *rufescens* Swainson, 1822
holzneri Hemphill, 1907: var. of *cracherodii* Leach, 1814 [66]
howensis (Iredale, 1929) [in *Sanhaliotis*]: *rubiginosa* Reeve, 1846 [43]
huttoni Filhol, 1880: ssp. of *virginea* Gmelin, 1791 [60]
imperforata Gmelin, 1791: *nomen dubium* [66]
imperforata Dall, 1919: homonym, *cracherodii* Leach, 1814 [66]
improbula Iredale, 1924: syn., var. of *rubra* Leach, 1814
incisa Reeve, 1846: *tuberculata* Linnaeus, 1758 [16]
interrupta Valenciennes, 1831: *nomen dubium* [73]
iridis Karsten, 1789: unavailable, *iris* Gmelin, 1791 [74]
iris Gmelin, 1791: valid [54]
jacnensis Reeve, 1846: valid [41]
janus Reeve, 1846: *tuberculata coccinea* Reeve, 1846 [17]
japonica Reeve, 1846: *tuberculata* Linnaeus, 1758 [16]
jousseaumi Mabille, 1888: *pustulata* Reeve, 1846 [11]
kamtschatkana Jonas, 1845: valid [62, 67]
kraussi Turton, 1932: *parva* Linnaeus, 1758
laevigata Donovan, 1808: valid
lamellosa Lamarck, 1822: var. of *tuberculata* Linnaeus, 1758 [5, 13]
latilabris Philippi, 1848: *ovina* Gmelin, 1791 [8]
lauta Reeve, 1846: *semiplicata* Menke, 1843 [49]
lucida Requien, 1848: *tuberculata* var. *lamellosa* Lamarck, 1822
lusus Finlay, 1927: var. of *cracherodii* Leach, 1814 [66]
maculata Küster, 1840. *nomen dubium* [18]
maculosa Küster, 1840: *nomen dubium* [18]
madaka (Habe, 1977) [in *Nordotis*]: valid [64]
mariae Wood, 1828: valid [26]
marmorata Linnaeus, 1758: valid [4, 5, 6]
marmorata Reeve, 1846: homonym, *virginea* Gmelin, 1791
melculus (Iredale, 1927) [in *Marinauris*]: *brazieri* Angas, 1869 [35]
midae Linnaeus, 1758: valid [04]
modesta auct.: *nomen nudum* ?, *midae* Linnaeus, 1758 [75]
morioria Powell, 1938: ssp. of *virginea* Gmelin, 1791 [60]
multiperforata Reeve, 1846: *rugosa* Lamarck, 1822 [32]
naevosa Philippi, 1844: *rubra* Leach, 1814 [54]
nebulata Reeve, 1846: *rugosa* Lamarck, 1822 [33]
neglecta Philippi, 1848: valid ? [5, 8, 9]
nodosa Philippi, 1845: *corrugata* Wood, 1828
ovina Gmelin, 1791: valid
oweni Talmadge, 1966: var. of *corrugata* Wood, 1828
papulata Reeve, 1846: var. of *varia* Linnaeus, 1758
parma Valenciennes, 1831: *nomen dubium* [73]
parva Linnaeus, 1758: valid [4]
parva Risso, 1826: homonym, *tuberculata* var. *lamellosa* Lamarck, 1822
pellucida von Salis, 1793: *tuberculata* var. *lamellosa* Lamarck, 1822
pertusa Reeve, 1846: *rugosa* Reeve, 1846 [33]
picta Röding, 1798: *glabra* Gmelin, 1791
planata Sowerby, 1882: valid [42]
planilirata Reeve, 1846: *fulgens* Philippi, 1845 [47]
plicata Karsten, 1789: unavailable, *australis* Gmelin, 1791 [74]
plicata Gmelin, 1791: *nomen dubium*
ponderosa Adams, 1848: *rufescens* Swainson, 1822
pourtalesii Dall, 1881: valid [1, 2, 3]
pulcherrima Gmelin, 1791: valid
pustulata Reeve, 1846: valid [12]
pustulifera Pillsbry, 1890: *varia* Linnaeus, 1758
queketti Smith, 1910: valid
reticulata Reeve, 1846: *tuberculata* Linnaeus, 1758 [16]
revea Bartsch, 1940: *fulgens, nomen nudum*
revelata Deshayes, 1863: *rugosa* Reeve, 1846 [12]
roberti McLean, 1970: valid [2]
roedingi Menke, 1844: *squamosa* Gray, 1826 [29]
roei Gray, 1826: valid [27]
rosacea Reeve, 1846: *marmorata* Linnaeus, 1758 [6]
rosea Orcutt, 1900: *cracherodii* Leach, 1814
rotundata Perry, 1811: *nomen dubium* [22]
rubicunda Röding, 1798: *parva* Linnaeus, 1758 [20]
rubicunda (Montfort, 1810) [in *Padollus*]: homonym, *parva* Linnaeus, 1758 [20]
rubiginosa Reeve, 1846: valid [43]
rubra Leach, 1814: valid [25, 51]
rufescens Swainson, 1822: valid
rugosa Lamarck, 1822: valid [12]
rugosa Reeve, 1846: homonym, *tuberculata* Linnaeus, 1758
rugosoplicata Chemnitz, 1788: unavailable, *australis* Gmelin, 1791 [59]
rugosoplicata Reeve, 1846: *australis* Gmelin, 1791 [59]
sanguinea Hanley, 1840: *spadicea* Donovan, 1808 [21]
scalaris (Leach, 1814) [in *Padollus*]: valid [56]
scabricostata Menke, 1843: *roei* Gray, 1826
schroeteri Menke: *nomen dubium* [76]
scutulum Reeve, 1846: *varia* Linnaeus, 1758 ? [47, 48]
secernenda Monterosato: *tuberculata* var. *lamellosa* Lamarck, 1822
semiplicata Menke, 1843: valid
semistriata Reeve, 1846: *varia* Linnaeus, 1758
sepiculata Reeve, 1846: *diversicolor* Reeve, 1846 ?, *tuberculata* Linnaeus, 1758 ?
sieboldii Reeve, 1846: *gigantea* Gmelin, 1791 [64]
sinuata Perry, 1811: *spadicea* Donovan, 1808 ? [22]
smithsoni Bartsch, 1940: *kamtschatkana assimilis* Dall, 1878
sorenseni Bartsch, 1940: valid
spadicea Donovan, 1808: valid [21]
speciosa Reeve, 1846: valid
splendens Reeve, 1846: *fulgens* Philippi, 1845
splendidula Williamson, 1893: *cracherodii* Leach, 1814
squamata Reeve, 1846: valid
squamosa Gray, 1826: valid [27, 28]
stomatiaeformis Reeve, 1846: *squamata* Reeve, 1846 [39]
striata Linnaeus, 1758: *tuberculata* var. *lamellosa* Lamarck, 1822 [4, 13]
strigata Weinkauff, 1883: *marmorata* Linnaeus, 1758
subvirginea Weinkauff, 1883: *virginea* Gmelin, 1791
sulcosa Philippi, 1845: *roei* Gray, 1826
supertexta Lischke, 1870: var., syn. of *diversicolor* Reeve, 1846 [38]
tayloriana Reeve, 1846: var., syn. of *diversicolor* Reeve, 1846
tricostalis Lamarck, 1822 : *scalaris* Leach, 1814
tricostata Wood, 1828: *scalaris* Leach, 1814

tuberculata Linnaeus, 1758: valid [4, 5, 13]
tubifera Lamarck, 1822: *gigantea* Gmelin, 1791
turveri Bartsch, 1940: var. of *fulgens* Philippi, 1845
unilateralis Lamarck, 1822: valid [30]
varia Linnaeus, 1758: valid [4]
varia Risso: homonym, *tuberculata* var. *lamellosa* Lamarck, 1822 [4, 44]
venusta Adams and Reeve, 1848: *clathrata* Reeve, 1846 [24]
victoriae Brazier: *nomen nudum* ?, *rubra* Leach, 1814 [77]
virginea Gmelin, 1791: valid [60]
virginea Reeve, 1846: homonym, *marmorata* Linnaeus, 1758
viridis Reeve, 1846: *varia* Linnaeus, 1758
vixlirata (Cotton, 1943): *rubra conicopora* Péron, 1816 [53]
vulgaris da Costa, 1778: *tuberculata* Linnaeus, 1758
walallensis Stearns, 1898: valid
whitehousei (Colman, 1959) [in *Sanhaliotis*]: *rubra* Leach, 1814 [55]
zealandica Reeve, 1846: *coccinea* Reeve, 1846 [17]
ziczac Reeve, 1846: *glabra* Gmelin, 1791

NOTES:

01. *Haliotis barbouri* Foster, 1945, has been a very controversial species. It was described from a single, beach shell from the coast of Brazil. It has been hypothesized that is is either a distinct species, or a mislocated specimen of either *H. pourtalesii* Dall, 1881, from the Caribbean (Rios, 1975) or the only Polynesian species, *H. pulcherrima* Gmelin, 1791 (Cox, 1962; Rios, 1985, 1994). *Haliotis barbouri* has not been included in the discussion of Brazilian Haliotidae by Simone (in press). Klappenbach (1968) mentioned a living specimen taken off Brazil, refuting the claim the species represents speciments left by tourists (*cf.* Cox, 1962). Specimens of *H. pourtalesii* have been indicated from the Gulf of Mexico to as far south as Venezuela and Brazil (Henderson, 1915; Foster, 1946; Aguayo and Jaume, 1947; Harry, 1966; Guice, 1968; Klappenbach, 1968; Sarasúa, 1968; Nijssen-Meyer, 1969; Titgen and Bright, 1985; Odé, 1986; Martinez and Tuiz, 1994). The more southern reports of *H. pourtalesii* including Klappenbach's (1968) live specimens can be attributed to confusion with a new species described (Simone, in press).
    Inspection of the type of *H. barbouri* (MCZ 152469) revealed its true identity as a somewhat aberrant form of *H. varia* Linnaeus, 1758. At a size of 22 mm it is a rather small specimen for the species. In general, small specimens of abalone tend to be rounder than larger ones (*cf.* Stewart and Geiger, in press: fig. 4). Hence, based on the overall shape of the shell one may be led to regard the type of *H. barbouri* as closely related to *H. pulcherrima*. However, the sculpture differs greatly. Most significantly, in *H. pulcherrima* a narrow spiral band adjacent to the row of tremata and devoid of oblique radial elements is found near the suture. A similar band is present in *H. jacnensis* Reeve, 1846 (*cf.* Figure 16, note 41). In *H. varia* and the type of *H. barbouri* this bare space is absent. The type of *H. barbouri* somewhat evokes the type specimens of *H. gemma* Reeve, 1846 (= *H. varia*: see note 46) in terms of size, rotundity, and sculptural elements.
02. *Haliotis dalli* Henderson, 1915, and *H. roberti* McLean, 1970, are two small, insular species found offshore from Central America at the Galapagos Islands (*H. dalli*) and Cocos Island (*H. roberti*). The two species are fairly similar but can be distinguished as indicated by McLean (1970). Radulae of both species share a very narrow lateral tooth 1 and concentric rings on the cephalic tentacles. These characters are shared only with *H. pourtalesii* Dall, 1881, and the new species to be described from Brazil (Simone, in press), but is not seen in any of the other 30 abalone species studied so far (Geiger, pers. obs.).
03. The neotype of *H. pourtalesii* Dall, 1881, is now broken in many pieces. The original illustration of the neotype (Henderson, 1915: pls. 45–46) showed an intact shell.
04. When Linnaeus (1758) introduced the first seven haliotids (*H. asinina, H. marmorata, H. midae, H. parva, H. striata, H. tuberculata, H. varia*), the concept of type specimens was not yet established. The LSL holds specimens in the collection, and I agree with Talmadge (1977a) that most correspond well with the current concept of the respective species. Talmadge (1977a) noted a single specimen of *H. tuberculata*, whereas I found six specimens with a note by S. P. Dance from 1963, also referring to six specimens. No specimens are currently designated as types. As indicated by Talmadge (1977a), there is no specimen of *H. parva* in the LSL. Designation of a neotype is unnecessary because the species does not present any nomenclatural problems (ICZN Article 75b).
05. The *H. tuberculata* group contains the following main taxa: *H. tuberculata* Linnaeus, 1758, *lamellosa* Lamarck, 1822, *coccinea* Reeve, 1846, *bistriata* Gmelin, 1791, and possibly also *H. marmorata* Linnaeus, 1758 (*cf.* Talmadge, 1963a) (Figures 18–19) and *H. neglecta* Philippi, 1848 (Figures 20–21). Of the well-known taxa in the group *H. tuberculata* was the earliest to be named; the group name is attributed to this species. All the species are found in Europe and northwest Africa (Mediterranean, Brittany to São Tomé and Gabon, Canary Islands, Azores). cDNA analysis of the protein lysin (Lee and Vacquier, 1995) has shown that *tuberculata* and *lamellosa* from the Mediterranean are the same species. The *tuberculata* and the *lamellosa* forms are usually found within one population (Geiger, pers. obs.). The taxon *lamellosa*, therefore, refers to a variety or ecomorph of *H. tuberculata*. *Haliotis coccinea* was shown to be closely related to *H. tuberculata* (Lee and Vacquier, 1995). It differs form *H. tuberculata* in only four positions of the 132 amino acid sequence whereas most species differ in ap-

proximately 15–20 amino acid positions. Despite the small difference in amino acid sequence, the shells are readily distinguishable and *H. coccinea* is found only at the Canary Islands. Two conditions warranting the subspecific status of *H. tuberculata coccinea* are present: distinct character and specific geographic location. From shell morphology observations, *H. bistriata* seems to be a variation of *H. tuberculata sensu lato* (see note 14). *Haliotis marmorata* Linnaeus, however, seems to be distinct in terms of shell morphology (Figures 18–19), but neither anatomical characters, nor biochemical data are available. Its status in relation to *H. tuberculata* remains unresolved.

06. The specimens labeled *H. marmorata* Linnaeus, 1758, are conspecific with what is best known as *H. rosacea* Reeve, 1846. This latter has been synonymized with *H. guineensis* Gmelin, 1791 (Talmadge, 1963b; Ubaldi, 1987) (Figures 18–19). Despite the possibility of exchange of material (K. Way, pers. comm.), three lines of evidence suggest that the specimens are likely to represent the species as described by Linnaeus: 1) Sowerby (1882) already indicated the synonymy between *H. marmorata* Linnaeus, *H. rosacea,* and *H. guineensis* (explanation to plate 11, figs. 88, 89); 2) some old specimens of this species labeled *H. marmorata* Linnaeus have been found in collections (*e.g.*, DMNH 011036); 3) S. P. Dance stated on a label from 1963 that "from several undocumented shells I have selected one that matches specimens in Brit. Mus. (Nat. Hist.) labeled '*H. rosacea* Reeve.' This is almost certainly the example mentioned by Hanley as present." Therefore, the correct name for the continental west African species is *H. marmorata* Linnaeus. Talmadge (1977a), in his discussion of Linnean haliotids, erroneously synonymized *H. marmorata* Reeve (*non* Linnaeus) with *H. virginea* Reeve (*non* Gmelin). *Haliotis marmorata* Reeve is clearly *H. virginea* Gmelin from New Zealand and not *H. marmorata* Linnaeus (= *H. virginea* Reeve) from west Africa.

07. *Haliotis decussata* Philippi, 1850, was described in Philippi's (1847–1851) third volume, with the date of the volume given as 1851. However, the pages with the description of *Haliotis* are dated April 1850, which is the correct date.

08. Philippi referred to figure 4 for his *H. latilabris* Philippi, 1848, and figure 5 for *H. neglecta* Philippi, 1848; this is obviously an error and one should consult figures 5 and 4 for these species, respectively. Pickery (1991) indicated 1851 as publication date, but the species had been already described by Philippi (1848:16) prior to that date.

09. Philippi's (1847–1851) illustration of *H. neglecta* Philippi, 1848, is similar to green and brown mottled *H. squamata* Reeve, 1846, which led Sowerby (1882: 27) to synonymize these two taxa: ". . . *H. neglecta* of Philippi . . . is undoubtedly identical with our present species [*H. stomatiaeformis*]" (see also note 39). However, the type locality of *H. neglecta* is Sicily in the Mediterranean Sea, whereas *H. squamata* is an Australian species. Ubaldi (1987) indicated this species as being distinct, occurring on islands close to Sicily, Malta and Lampedusa, but without illustrating any specimens. Some specimens that correspond very well to the figured specimen have been located: one in MNHN (Sicily and Palermo), four in HUJ (6313a, b: Lampedusa and Giardini), one in DMNH (097371: near Malta Island), and one in my personal collection (Malta: Figures 20–21). *Haliotis tuberculata* Linnaeus, 1758, with the form *lamellosa* Lamarck, 1822, is the only native, well known, and highly variable species in the Mediterranean. *Haliotis neglecta* might just represent aberrant specimens of *H. tuberculata* (*cf.* Weber, 1928). However, the specimens I have seen are very distinct and unlikely to be only a variation of *H. tuberculata.* I consider *H. neglecta* to be a valid species, but it would be desirable to compare the epipodium, the radula, and DNA sequence data.

Interestingly, a similar case is found in the Conidae. *Conus ventricosus* Gmelin, 1791, is a species living throughout the Mediterranean. In the Sicily Channel area, *C. vayssieri* Pallary, 1906, is present (Villa, 1985), but this species has also been regarded as a mere form of *C. ventricosus* (Poppe and Goto, 1991).

10. *Haliotis pustulata cruenta* Reeve, 1846, migrated from the Red Sea into the Mediterranean Sea through the Suez Canal. It has been found along the Israeli coast (Talmadge, 1971; Fainzilber, 1984) and in Lybia (Giannuzzi-Savelli *et al.,* 1994). One alcohol-preserved specimen without the shell from Greece shows a more or less identical epipodium when compared to specimens of *H. pustulata cruenta* from the Red Sea. This latter is rather different from *H. tuberculata* Linnaeus, 1758, from the Mediterranean. It is, therefore, possible that this species has advanced further into the eastern Mediterranean. The few reports in the literature of this migrant species in contrast to others—*e.g., Strombus decorus* (Röding, 1798) (see *e.g.,* Fischer, 1993; Lindner, 1993)—may be due to the fact that the shells of the Red Sea species often are not strikingly different from the native *H. tuberculata.*

11. The geographic provenance of *H. jousseaumi* Mabille, 1888, was not given in the original description (Mabille, 1888), but the label of the specimen held in the MNHN cites the Red Sea ("Mer Rouge"). The name has only been used once thereafter by Talmadge (1956), who correctly synonymized it with *H. pustulata* Reeve, 1846.

12. A lectotype for *H. revelata* Deshayes, 1863, is here selected (see main body of text, Figures 8–9). The specimens are conspecific with what is better known as *H. rugosa* Lamarck, 1822. Herbert (1990) speculated about the synonymy between *H. pustulata* Reeve, 1846, and *H. rugosa* Lamarck, something

that had already been hinted by Wagner and Abbott (1978) in their synonymization of *H. alternata* Sowerby, 1882, with *H. pustulata*. I have not seen any material that has intermediate characters, and question the synonymy between the two taxa. The taxa *cruenta* Reeve, 1846, and *pustulata* may eventually be treated as a subspecies of *H. rugosa* Lamarck, pending further clarification based on their respective anatomies, but I tentatively consider them as here a distinct species (*cf.* Herbert, 1990; Geiger, 1996).

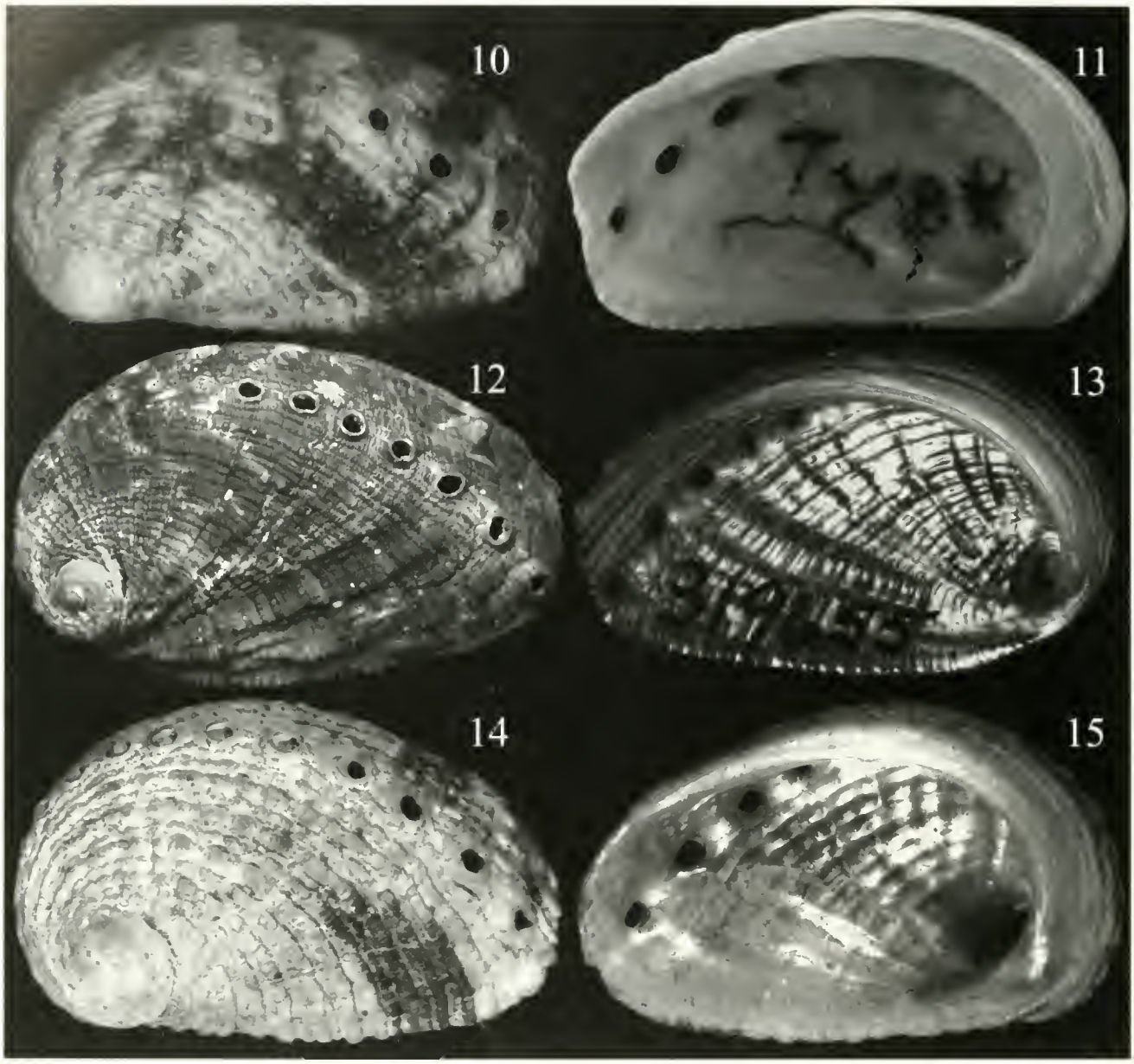
13. *Haliotis striata* Linnaeus, 1758, belongs in the *H tuberculata* Linnaeus, 1758 group (see note 5). I agree with Talmadge (1977a) that it corresponds with what is well known as *H. tuberculata* var. *lamellosa* Lamarck, 1822 (Figures 28–29). If *H. tuberculata* is a synonym of *H. lamellosa*, then *H. striata* is also a synonym of *H. tuberculata*. *Haliotis tuberculata* is preferred over *H. striata* as the valid name for the species because it is the established name. However, if taxonomic distinction between *H. tuberculata* and *H. lamellosa* is favored, then *H. striata* has priority over *H. lamellosa*. Suppression of *H. striata* would be desirable, as previously suggested by Pilsbry (1890:87).
14. Weber (1928) mentioned the extensive variability of *H. bistriata* Gmelin, 1791, from Tenerife, Canary Islands, some of which correspond with its original description, some that are typical *H. tuberculata* Linnaeus, 1758, and concluded that the two taxa are most likely conspecific. He did not mention *H. coccinea* Reeve, 1846, and possibly was synonymizing too much under one taxon (see also note 9). The taxon *bistriata* is mostly encountered in the old literature, and a few specimens from old collections labeled *H. bistriata* could be found in the BMNH and ANSP. Most of the specimens that show some resemblance to old illustrations (*e.g.*, Reeve, 1846: pl. 11, fig. 33) originated from the Canary Islands and the Azores. The specimens are characterized by strong radial grooves and a flared aperture. A separation of *H. bistriata* from other members of the *H. tuberculata* group (see note 5) cannot be accepted. The localities, illustrations, and specimens labeled as *H. bistriata* do not show any coherent pattern. *Haliotis bistriata* should be regarded as a growth form of either *H. tuberculata coccinea* for specimens from the Canary Islands and the Azores, or of *H. tuberculata* or *H. marmorata* in the case of specimens from the East Atlantic mainland. As *H. bistriata* most likely refers to three different species-level taxa, I prefer to treat it as a *nomen dubium*, which further provides stability to the nomenclature, because the populations from the Canary Islands are well known under the epithet *coccinea*.
15. *Haliotis bisundata* Monterosato is listed as a variety of *H. tuberculata* Linnaeus, 1758, in Priolo (1948) and Ghisotti (1964), but cannot be traced.
16. *Haliotis incisa* Reeve, 1846, *H. japonica* Reeve, 1846, and *H. reticulata* Reeve, 1846, are all reported from Japan. This type locality is questionable and the type specimens look exactly like the Mediterranean *H. tuberculata* Linnaeus, 1758, as also indicated by Reeve (1846) and discussed in Dunker (1882), Weinkauff (1883), McLean (1966), and Kaicher (1981: card no. 2882). Weinkauff (1883:59) nevertheless reported for *H. japonica* similar specimens "without any doubt" from Japan, but not giving the locality record more credibility. In modern times no similar specimens have been reported from the well-studied area of Japan. *Haliotis japonica* and *H. tuberculata* var. *lamellosa* Lamarck, 1822, have also been synonymized erroneously (Pilsbry, 1890:87) with *H. aquatilis* Reeve, 1846, this latter being a synonym of *H. diversicolor* Reeve, 1846.
17. The epithet *coccinea* Reeve, 1846, is assigned as a subspecies of *H. tuberculata* Linnaeus, 1758. This is here established after examination of cDNA sequencing data (Lee and Vacquier, 1995), distinct shell characters, and its isolated geographic occurrence at the Canary Islands (see also note 5). *Haliotis janus* Reeve, 1846, is a color form of *H. tuberculata coccinea* (Talmadge, 1958).
18. *Haliotis maculata* Küster, 1840, and *H. maculosa* Küster, 1840, (spelling variations?) are mentioned by Sowerby (1882:36, pl. 9) and Weinkauff (1883: 83) as senior synonyms of *H. coccinea* Reeve, 1846. The name is based on figure 137 in Martini and Chemnitz (1769) (non-binominal), which shows very clearly *H. tuberculata coccinea* (see note 17). The original source could not be traced, and Küster's taxa were not listed in Sherborn (1922; 1932). According to Weinkauff, Küster's name has priority over Reeve's, an opinion not followed here, because the citation of Küster's work could not be located.
19. The type specimen of *H. canaliculata* Fischer, 1807, was lost prior to 1872 (Ivanov and Kantor, 1991). Fischer (1807) indicated the presence of a deep, spiral canal and a brownish shell with many spiral cords in this small species. These characters point toward *H. parva* Linnaeus, 1758, a species to which he did not refer. The synonymy is tentative.
20. *Haliotis rubicunda* (Montfort, 1810) has also been attributed erroneously to Gray (1826) (see also note 27). Gray clearly referred to Montfort. Montfort used this species as type species for his genus *Padollus* and did not refer to any other author, which makes it likely to be a new taxon introduced by him and not *H. rubicunda* Röding, 1798 (synonym of *H. parva* Linnaeus, 1758). *Haliotis rubicunda* (Montfort) was inflected to the masculine by Montfort for his new genus *Padollus* (see Knight *et al.*, 1960; Pickery, 1991; also Schremp, 1981:1125). The type locality is the "African coasts." The key feature of the species is the spiral ridge on the shell; a character seen only in *H. parva* among the African species (Iredale, 1927:334). *Padollus rubicundus* Montfort has also been synonymyzed with *H. scalaris*

(Leach, 1814) (see also note 56), a species that, however, occurs only in Australian waters. Because *H. rubicunda* Röding and *P. rubicundus* Montfort refer to the same species, they must belong to the same genus, for which the species have to take the correct generic ending of the adjectival species name, causing *P. rubicundus* Montfort either way to become a secondary homonym. Note that although *Padollus* is based on an invalid name, this does not make *Padollus* itself invalid.

21. *Haliotis sanguinea* Hanley, 1840, was reported also to have been described in 1808, in the same year as the senior synonym *H. spadicea* Donovan, 1808. Muller (1986) discussed the date of publication of *H. sanguinea* at length and concluded that it was actually described in 1840.
22. The descriptions of *H. rotundata* Perry, 1811, and *H. sinuata* Perry, 1811, given by Perry (1811: pl. 52) are very brief and general, and his figures are rather stylistic. Pilsbry (1890) listed both as unidentified species. The undulation of the apertural margin as well as the general shape of the shell of *H. sinuata* is reminiscent of *H. spadicea* Donovan, 1808.
23. *Haliotis clathrata* Lichtenstein, 1794, has so far been considered a *nomen dubium* (Wagner and Abbott, 1978). This causes *H. clathrata* Reeve, 1846, to be an invalid, junior, primary homonym. *Haliotis clathrata* Lichtenstein is discussed by Geiger in press and identified as *H. elegans* Philippi, 1844. Geiger and Stewart (under consideration) have petitioned the International Commission on Zoological Nomenclature to suppress *H. clathrata* Lichtenstein to preserve *H. elegans* and *H. clathrata* Reeve. This position, pending decision by the Commission, is provisionally adopted here (ICZN Article 80).
24. *Haliotis venusta* Adams and Reeve, 1848, has so far been considered distinct from *H. clathrata* Reeve, 1846, due to the absence of radial lamellae on the type specimens. Several characters can be observed on both series of type specimens of *H. clathrata* Reeve and *H. venusta* (1 holotype, 2 paratypes each in BMNH): 1) a pattern of approximately 4–5 faint growth lines followed by one stronger one; 2) tremata only slightly oval, but rather large in comparison to the shell; 3) all shells of orange and white color, despite some fading; 4) in both series, some specimens with spire fully visible in ventral position, some only partially; 5) numerous spiral cords; 6) usually three to four of these cords stronger than others; stronger cords regularly spaced between suture and row of tremata; 7) the Indo-Pacific type localities for both taxa: Baclayon, Island of Bohol, Philippines for *H. clathrata* Reeve, and Eastern Seas for *Haliotis venusta*. *Haliotis clathrata* Reeve is distinguished from *H. venusta* by the discrete, numerous radial lamellae in the respective holotypes. The lamellae of *H. clathrata* Reeve are formed along the stronger growth lines, *i.e.*, every four to five faint growth lines. The lamellae of *H. clathrata* Reeve represent elevated, strong growth lines in *H. venusta*, hence the two structures are homologous. Radial lamellae are known to appear randomly in populations of a single species of *Haliotis*. The best documented case is that of *H. tuberculata* Linnaeus, 1758, from the Mediterranean, where the lamellate form is well-known as *H. lamellosa* Lamarck, 1822, *H. tuberculata lamellosa*, or *H. tuberculata* form *lamellosa* (Ubaldi, 1987; Poppe and Goto, 1991). In a large series of over 400 specimens all intermediate forms could be found within any given population (Geiger, unpubl. data). The two taxa have been shown to have an identical caryotype (Colombera and Tagliaferri, 1983) and an identical cDNA sequence of the acrosomal sperm protein lysin (Lee and Vacquier, 1995). Although the material for *H. clathrata* Reeve and *H. venusta* is not as abundantly available as for the Mediterranean species, I am convinced that a similar case can be made for the Indo-Pacific taxa in question. I, therefore, synonymize *H. venusta* under *H. clathrata* Reeve.
25. *Haliotis crebrisculpta* Sowerby, 1914, has been synonymized with *Haliotis clathrata* Reeve, 1846 (Kuroda and Habe, 1952). It has also been listed as a subspecies of *H. rubra* Leach, 1814 (Talmadge, 1957b). Both opinions are rejected; the validity of the species is discussed in Stewart and Geiger (in press) and the reader is referred to this work for an in-depth treatment (see also note 36).
26. *Haliotis corrugata* Wood, 1828, has also been attributed to Gray. However, Wood (1828) published a figure with the name of *H. corrugata* in the supplement to his *Index Testaceologicus*. Gray apparently supplied some of the material, on which the figures were based (p. iiv of Supplement), but Wood actually published the figure; he is consequently the author of the taxon.
27. Serious confusion about the date of publication of Gray's (1826) work is found in the literature. The publication dates indicated are 1826 and 1827. The work was edited in two volumes, where volume 1 is dated 1827, but one copy of volume 2 that I have seen is dated 1826 and another copy is dated 1827. Generally, 1826 is accepted as the correct date, because it is the earliest confirmed date of publication.
28. *Haliotis squamosa* Gray, 1826, was erroneously described from Australia, but actually occurs in a restricted area in southern Madagascar. The species was rediscovered in Madagascar by Dautzenberg (1932) and again by Stewart (1984).
29. *Haliotis roedingi* Menke, 1844, was described by Menke (1844:97) in "2 neue *Haliotis* Arten, beschrieben vom Herausgeber" (2 new species of *Haliotis*, described by the editor). According to Menke, the species was already known and named by Chemnitz; Menke gave the name "*Haliotis Roedingi*, Chemn." It is clear that the species was known to Chemnitz, but was described by Menke. Based on the description as well as the locality (*cf.* Pilsbry,

1890: 112, note 28), I agree with Stewart (1984) that Menke, 1844, is the author and that *H. roedingi* is a synonym of *H. squamosa* Gray, 1826.

30. The taxonomic status of *Haliotis unilateralis* Lamarck, 1822, has been much disputed (Figures 32–33). Geiger (1996) designated a neotype and discussed the taxon in detail. Menke (1830:88) listed this species. Mention of the species in Casto de Elera (1896) in his catalog of shells from the Philippines is questionable. This latter author also mentioned species known at the time not to occur on the Philippine Islands. The best example is *H. mariae* Wood, 1828, a species endemic to Oman.
31. Sowerby's abalone taxa from the *Thesaurus Conchyliorum* have been dated 1883 (Abbott and Dance, 1983) or 1887 (Pickery, 1991). The individual volumes were issued in a number of parts (*cf.* British Museum (Natural History), 1915). Volume 5 was published between 1882 and 1887. The haliotids appeared in the first part of Volume 5 in 1882, which is the correct date for these taxa. It is not a printing date, as most taxa are listed in the *Zoological Record* of 1882 (Martens, 1882).
32. A lectotype for *H. multiperforata* Reeve, 1846, is here selected (see main body of text, Figures 6–7). The synonymy with *H. spadicea* Donovan, 1808 (see Wagner and Abbott, 1978) is certainly wrong.
33. *Haliotis pertusa* Bartsch, 1915, and *H. nebulata* Turton, 1932, are indicated in Barnard (1963) as synonyms of *H. spadicea* Donovan, 1808. I assume that Barnard intended to indicate *H. pertusa* Reeve, 1846, *sensu* Bartsch (1915) and *H. nebulata* Reeve, 1846, *sensu* Turton (1932). The types of *H. pertusa* and *H. nebulata* are clearly referable to *H. rugosa* Lamarck, 1822 (see also note 12).
34. *Haliotis hargravesi* Cox, 1869, and *H. ethologus* (Iredale, 1927) are uncommon to rare in southern Queensland and northern New South Wales. Whitehead (1981:5) specifically noted for *H. hargravesi* that "known localities are as for *H. ethologus.*" The only distinguishing characters between these two taxa is the number of spiral ribs and their elevation. However, these characters seem to be rather variable, pointing to extensive intraspecific variability, and indicating presence of a single, polymorphic species. The two taxa represent slight variations within the morphological range when a large enough sample is examined.
35. The type of *H. melculus* (Iredale, 1927) is severely chipped, has very elevated tremata and hardly any spiral ribs: it suggests *H. brazieri* Angas, 1869. Wilson (1993) figured a specimen with many thin spiral threads as *H. melculus*. I regard it as a specimen in the *H. hargravesi* Cox, 1869—*brazieri* continuum (see also note 34 and Hybrids section above).
36. For *H. crebrisculpta* Sowerby, 1914, three syntypes are known in the BMNH, the NMW, and in the USNM. The specimen in the BMNH is very similar to the figured specimen in Sowerby (1914); the specimens in the NMW and the USNM represent *H. clathrata* Reeve, 1846 (see notes 24, 25). The specimen in the BMNH has been designated as the lectotype (Stewart and Geiger, in press). *Haliotis dissona* (Iredale, 1929) is here considered a valid species (*cf.* note 39; Figures 10–11), although Whitehead (1981) listed it as a synonym of *H. crebrisculpta*. *Haliotis dissona* has also been synonymized by Wagner and Abbott (1978) with *H. diversicolor* Reeve, 1846, and its forms (Figures 12–13), an opinion I strongly oppose. The characters common to *H. dissona* and *H. diversicolor* (more or less smooth shell with spiral ridges) are due to the type specimen of *H. dissona* being badly worn and rather small. The distinct elongated shape of the shell of *H. dissona* with rather deep spiral ridges and grooves in fresh specimens sets it apart from *H. diversicolor*. The illustration of Iredale (1929) exaggerated the sculpture of the shell to a great extent; it may be considered a reconstructive drawing of a fresh shell from a worn specimen.
37. *Haliotis diversicolor* Reeve, 1846, is well known from the temperate northwestern Pacific, from central to southern Japan (Lindberg, 1992) and somewhat further south. The species has now been found in a small number of independent lots from Bali and New Caledonia, but only from localized upwelling areas (Figures 12–13). Upwelling areas are thought to exist on many of the surrounding islands that may provide habitat for this temperate species (S. A. Shepherd, pers. comm.). The shells are more elongated in general shape than typical ones, and are as highly arched as *H. squamata*. Additionally, they are mostly of uniform, dark sepia coloration, which may be interpreted as a case of melanism. Melanistic shells are well known in some gastropods such as in the Cypraeidae, and New Caledonia is known for a higher frequency of such dark colored specimens. Whether these tropical populations of *H. diversicolor* represent refugia or have only been colonized in geologically recent time is not known. A taxonomic separation seems inappropriate.
38. Two spelling variations are found in the literature: *H. supertexta* Lischke, 1870, and *H. supratexta*. The original spelling was *H. supertexta*.
39. Talmadge (1962) treated *H. stomatiaeformis* Reeve, 1846, as a subspecies of *H. varia* Linnaeus, 1758. I disagree with his conclusion after inspection of the type material: *H. stomatiaeformis* is a typical *H. squamata* Reeve, 1846 (see note 57). Specimens normally identified as *H. stomatiaeformis* are usually referable to *H. dissona* (Iredale, 1929) (*cf.* note 36).
40. *Haliotis dohrniana* Dunker, 1863, is a little known species with distinct affinities to *H. varia* Linnaeus, 1758, as already indicated by Dunker (1870:7). The epipodium shows distinct characteristics (Geiger, pers. obs.).
41. *Haliotis hanleyi* Ancey, 1881, and *H. jacnensis* Reeve, 1846, have been considered to be distinct

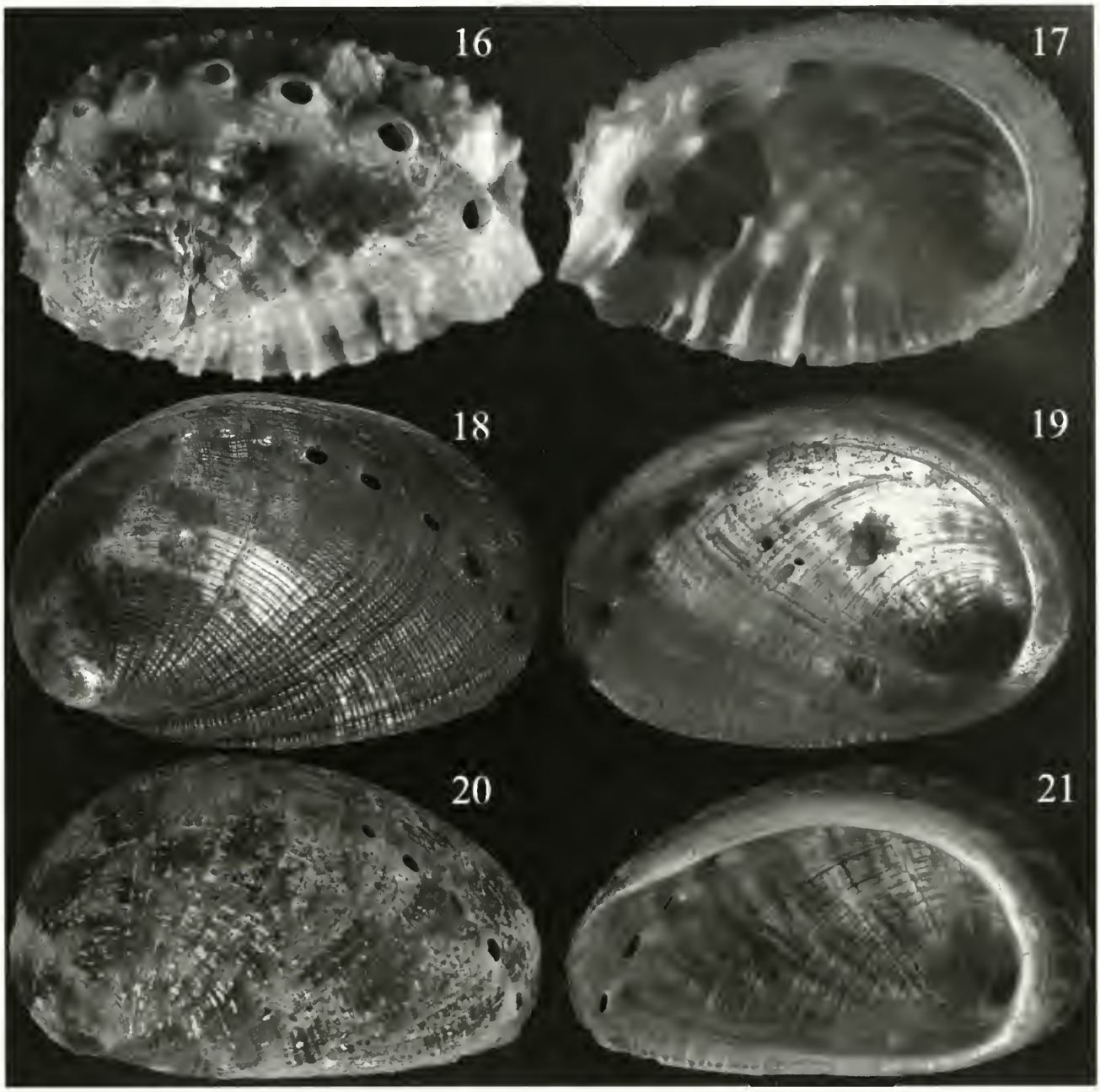


Figures 10–15. Infrequently illustrated *Haliotis*. 10–11. *Haliotis dissona* (Iredale, 1929). 33 mm. R. Pickery collection. New Caledonia. **12–13.** *H. diversicolor* Reeve, 1846. 30 mm. ANSP 319655. Bali Beach Hotel. **14–15.** *H. exigua* Dunker, 1877. 21 mm. NMW 1955. 158. 2133. Japan.

species (*e.g.*, Talmadge, 1963a; Kaicher, 1981). The distinguishing characters were thought to be the general shape of the shell, and the extent to which the shell bears cords. These characters are highly variable and the two taxa represent slight variations within the morphological spectrum of one biological species. The geographical distribution of the two taxa is congruent. The smooth, dorsal part of the shell proximal to the row of tremata is a synapomorphy with *H. pulcherrima* Gmelin, 1791 (see note 1), and a diagnostic character of the species (Figures 16–17).

42. Sowerby indicated Carpenter as authority for *H. planata* Sowerby, 1882. Weinkauff (1883:76) could not find the source; he indicated "*ubi*?" (Latin for 'where?'). Today Sowerby is usually credited with the authorship of the taxon. *Haliotis planata* is occasionally confused with *H. varia* Linnaeus, 1758. I agree with Talmadge (1963a) that distinctive epipodial morphologies separate the two species.

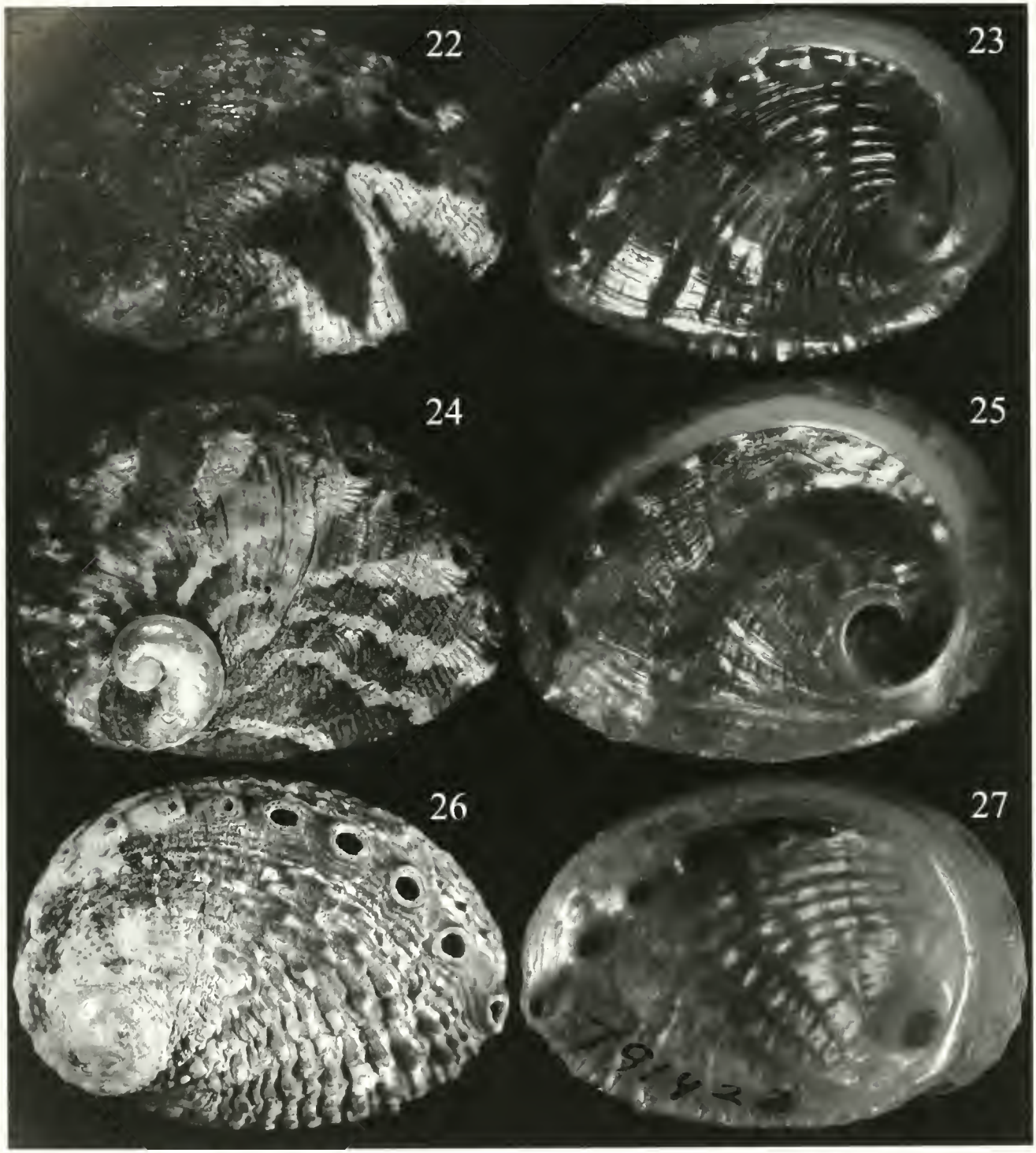
43. *Haliotis rubiginosa* Reeve, 1846, has most often been used as a synonym, form, or subspecies of *H. varia* Linnaeus, 1758 (*e.g.*, Kaicher, 1981). *Haliotis howeusis* (Iredale, 1929) was described and is endemic to Lord Howe Island. Old specimens labeled as *H. rubiginosa* from Lord Howe Island were lo-



Figures 16–21. Infrequently illustrated *Haliotis*. 16–17. *Haliotis jacnensis* Reeve, 1846. 12 mm. R. Pickery collection. No location data. **18–19.** *H. marmorata* Linnaeus, 1758. 63 mm. LSL. *Mare africanus*. **20–21.** *H. neglecta* Philippi, 1848. 29 mm. Collection Geiger AAB 51a. Malta Island.

cated in the BMNH (K. Stewart, pers. comm.) and in the HUJ (12557). The types of the two species are very similar, and I agree with K. Stewart that the two names refer to the same species. *Haliotis rubiginosa* has priority over *H. howensis*, despite the latter being better known (Figures 26–27).

44. The type locality of *H. varia* Linnaeus, 1758, is Philippine Islands as designated by Iredale (1910).
45. It is unclear whether or not *H. dringii* Reeve, 1846, represents a distinct species or a form of *H. varia* Linnaeus, 1758. As *H. varia* is such a variable species, I am inclined to synonymize *H. dringii* under *H. varia*. Many specimens identified in collections as *H. dringii* are actually *H. jacnensis* Reeve, 1846 (Figures 16–17).
46. *Haliotis gemma* Reeve, 1846, is quite certainly a color form of *H. varia* Linnaeus, 1758, as seen from the series of four type specimens in the BMNH, with one specimen marked "type." The synonymization is not entirely certain as the shells are rather



Figures 22–27. Infrequently illustrated *Haliotis*. **22–23.** *Haliotis planata* Sowerby, 1882. **22.** 39 mm. NMW 1955. 158. 2124. Philippines. **23.** 33 mm. NMW 1955. 158. 2125. Guadalcanal. **24–25.** *H. queketti* Smith, 1910. 33 mm. NMW 1955. 158. 2129. Pondoland. **26–27.** *H. rubiginosa* Reeve, 1846. 25 mm. USNM 791422. Lord Howe Island

small; juvenile abalone are notoriously difficult to identify, and *H. varia* is an extremely variable species. The selection of the specimen labeled "type" is questionable because the measurements of the shells and the indications in the description of the species do not match. The illustration of *H. gemma* is "magnified double" and the illustration is 19. 5 mm long; hence, the corresponding specimen should be a little less than 10 mm long. The specimen labled "type" measures 20. 5 mm, which is

twice the size of the original specimen. I believe that the reference to "magnified double" in the original description was incorrect. Kaicher (1981) illustrated another, unidentifiable specimen as *H. gemma*.

47. I found no type specimens for *H. planilirata* Reeve, 1846, or *H. scutulum* Reeve, 1846, in the BMNH. Talmadge (1964) indicated a type of *H. planilirata* in the BMNH.
48. From the description "waved, here and there larger," the coloration "olive brown . . . dotted and spotted with green," and the irregular spiral ridges with occasional thickenings to be seen in the figure 64 of Reeve (1846), I tentatively identify *H. scutulum* Reeve, 1846, as *H. varia* Linnaeus, 1758 (*cf.* note 47).
49. *Haliotis lauta* Reeve, 1846, was tentatively placed in the synonymy of *H. coccoradiata* Reeve, 1846, by Talmadge (1960). After inspection of the type specimens of both species in the BMNH, it is clear that the two taxa are not synonymous. I agree with other authors that *H. lauta* represents *H. semiplicata* Menke, 1843.
50. The authorship of *H. elegans* has also been indicated as "Koch *in* Philippi" (*e.g.,* Wells and Bryce, 1985: 34). The date printed on the description page of *H. elegans* is June 1844. This is the correct date. Philippi (1842–1845) indicated Koch as a reference; however, it is apparent that Philippi actually wrote the description and that only a short note was taken directly from Koch. Accordingly, I consider Philippi, 1844, the author.
51. The taxon as described by Leach (1814: pl. 23) is *H. ruber*. The correct inflected spelling for this adjectival species epithet, however, is *H. rubra*. Both spellings are found in the literature.
52. *Haliotis ancile* Reeve, 1846, has been shown to be a juvenile *H. rubra* Leach, 1814 (Geiger, 1996; Stewart and Geiger, in press), and not a green form of *H. pustulata* Reeve, 1846 (*cf.* Talmadge, 1956), or *H. japonica* Reeve, 1846 (*cf.* Wagner and Abbott, 1978) (note 16).
53. *Haliotis conicopora* Péron, 1816, and *H. rubra* Leach, 1814, have been shown to be closely related on the basis of allozyme frequency data (Brown, 1993: 430): "*Haliotis conicopora* clustered with the three populations of *H. rubra*, with a maximum D of 0. 018. Similar genetic distances were found between all conspecific populations studied (0. 003 in *H. roei* and 0. 014 in *H. laevigata*)." Further on pages 430–431: "*Haliotis conicopora* appears to represent an allopatric population (Western Australian) of *H. rubra*, as originally suggested by Shepherd (1975) and noted by Brown and Murray (1992a)." However, the two taxa can readily be distinguished by the shell thickness (dependent upon wave energy of the habitat), coloration (a potential function of food availability), and the presence of strong spiral cords (somewhat variable in both taxa) on a bumpy dorsal shell surface in *H. rubra*. Additionally, *H. rubra* is found in southeastern Australia, whereas *H. conicorpora* occurs in southwestern Australia. The genetic data suggest conspecifity, but the shell and the disjunct geographical distribution indicate distinct taxa. Thus, there is some justification for subspecies recognition of *conicopora* under *H. rubra*, although this remains to be fully resolved.
54. *Haliotis iris* is credited either to Martyn (1784: *cf.* Sinclair, 1963), or to Gmelin (1791: *cf.* Pickery, 1991; Lindberg, 1992). *Haliotis pulcherrima* has mostly been attributed to Gmelin except by Cotton (1943), but *H. naevosa* exclusively to Martyn. All three taxa are figured and named in Linnean binominal nomenclature by Martyn. However, the work of Martyn has been invalidated by ICZN opinion 456 (ICZN, 1957). Martyn's taxa are, therefore, not available and are now credited to the author who thereafter mentioned the species for the first time, which is Gmelin (1791) for *H. iris*, and Philippi (1842–1845:147) for *H. naevosa*. Philippi's Volume 1 is dated 1845, but the page with the description of *H. naevosa* is dated "Juli 1844;" therefore, the latter is the correct date for *H. naevosa*.
55. Only a single specimen, *i.e.*, the holotype, of *H. whitehousei* (Colman, 1959) is known. It is considered by P. Colman (pers. comm.), who described the taxon, as a teratological specimen of *H. rubra* Leach, 1814. Despite regular collecting at the type locality, no second specimen has ever been found (P. Colman, pers. comm.).
56. Intermediate specimens of *H. scalaris* (Leach, 1814) and *H. emmae* Reeve, 1846, are well known from western South Australia, indicating a close relationship between the two taxa (Shepherd, 1973; Wilson, 1993). The variability seems to be caused by the interplay of environmental factors such as wave energy, depth, and temperature (S. A. Shepherd, pers. comm). Subspecific status of the taxon *emmae* under *H. scalaris* is indicated, as the morphological gradient between the two taxa occurs only in a small geographical area, with the larger part of the species distribution showing only one of the morphologies.
57. The type specimen of *H. elevata* Sowerby, 1882, has not been found. The specimen was not figured in the standard dorsal and ventral position, but was tilted. However, it is evident from the dorsal sculpture and the eccentric spire that a small specimen of *H. squamata* Reeve, 1846, was illustrated. According to Sowerby (1882:27), it differs from *H. stomatiaeformis* Reeve, 1846 (syn. of *H. squamata*: see note 39), by having strong, scaly ridges, a character rather typical for juvenile specimens of *H. squamata* (Talmadge, 1955).
58. *Haliotis funebris* Reeve, 1846, was synonymized by Hedley (1914) with *H. diversicolor* Reeve, 1846, and *H. tayloriana* Reeve, 1846. My inspection of the type material in the BMNH shows that *H. funebris* is clearly a synonym of *H. squamata* Reeve, 1846 (see Pilsbry, 1890:92).

59. *Haliotis gigantea* Chemnitz, 1788, *H. glabra* Chemnitz, 1788, and *H. rugosoplicata* Chemnitz, 1788, are names that derive from the two first words of the original descriptions and that, therefore, cannot be interpreted as binominal names: the work and the authorship of these taxa are not available (ICZN, 1954). The names were validated by Gmelin (1791: *H. gigantea, H. glabra*) and Reeve (1846: *H. rugosoplicata*).
60. *Haliotis virginea* Gmelin, 1791, has been divided into four, geographically separated subspecies: *H. virginea virginea, H. virginea crispata* Gould, 1847, *H. virgina huttoni* Filhol, 1880, and *H. virginea morioria* Powell, 1938 (Kaicher, 1981; Ubaldi, 1986). Conflicting opinions are expressed as to whether these are valid subspecies (Powell, 1979; Ubaldi, 1986), or whether they would rather represent variations caused by differences in water temperature (Talmadge, 1957a). No good data are available to support either of the hypotheses; I retain usage of subspecific taxa.
61. *H. gibba* Philippi, 1846, is given as a synonym of *H. virginea* Gmelin, 1791, by Suter (1913), supported by the figures in Reeve (1846) and Weinkauff (1883).
62. Old specimens of *H. discus hannai* Ino, 1952, from Japan are usually identified on the original label as the North American *H. kamtschatkana* Jonas, 1845, to which it is strikingly similar. *Haliotis discus hannai* and *H. k. kamtschatkana* differ at the species level (Owen *et al.*, 1971; Brown, 1993; Lee and Vacquier, 1995).
63. *Haliotis exigua* Dunker, 1863, is usually encountered in material from the Ryukyu Archipelago (Figures 14–15). It has morphological affinities to both *H. varia* Linnaeus, 1758, and *H. diversicolor* Reeve, 1846. Pilsbry (1895) regarded *H. exigua* as a juvenile of *H. diversicolor*. The flat shells are rather nondescript, have an irregular sculpture, and are usually of a dark, muddy coloration. Whether these specimens deserve recognition at the species level is unclear. Inspection of preserved material would certainly help to resolve the status of this species.
64. The type specimen of *H. sieboldii* Reeve, 1846, is an aberrant specimen, as indicated *e.g.*, by Dunker (1882: 148): "Haec species mihi est valde dubia, . . . credam eam nil representare nisi conformationem Haliotis giganteae monstruosam." (This species is very doubtful to me, . . . I believe it does represent nothing but a grotesque form of *Haliotis gigantea*). The types of *H. sieboldii* and *H. gigantea* Gmelin, 1791, refer to the same species (Habe, 1983). The taxon *sieboldii* had long been used for a further species eventually named *H. madaka* (Habe, 1977). The two species can be distinguished as follows. In *H. gigantea* a line drawn through the apex of the shell and the last perforation results in very unequal areas of the shell, whereas the same line drawn in *H. madaka* divides the surface area of the shell approximately in half.

Haliotis gigantea Menke was mentioned in Weinkauff (1883:25) as published in Menke (1843), but Sherborn (1922) considered 1830 to be the year of publication of this taxon. Menke (1830:87; 1843:31) referred in both cases to *H. gigantea* Chemnitz, 1788, an unavailable name first mentioned thereafter by Gmelin (1791:3691), who listed this species from Australia ("*Habitat rarissima ad novam Holandiam*" [lives very rarely in Australia]). However, the type specimen of *H. gigantea* Gmelin, 1791, figured in Habe (1983) clearly shows the well-known northwest Pacific species. Due to the erroneous type locality, *H. gigantea* has been incorrectly synonymized with the common, commercially exploited *H. rubra* Leach, 1814, from southern Australia (*e.g.*, Menke, 1843).
65. The type specimen of *H. diegoensis* Orcutt, 1900, is a monstrosity induced by boring organisms, most likely sabellid polychaetes (see also Oakes and Fields, 1993).
66. Adult specimens with missing tremata have been reported occasionally in the literature. These represent deformations (see Leighton, 1960), rather than valid taxa. *Haliotis imperforata* Gmelin, 1791, may belong in this category or may be a misidentified, non-haliotid species. In the case of *H. imperforata* Dall, 1919 (*non* Gmelin, 1791), *H. lusus* Finlay, 1927, was proposed as a *nomen novum*. Finlay (1927), however, had overlooked the name *H. crachcrodii holzneri* Hemphill, 1907, which has priority.
67. *Haliotis assimilis* Dall, 1878, is a subspecies of *H. kamtschatkana* Jonas, 1845, as discussed by McLean (1966).
68. *Haliotis corcanica* Weinkauff, 1883, is mentioned in Habe and Kosuge (1964) and Habe (1983) as a synonym of *H. gigantea* Gmelin, 1791. This synonymy is based, however, on a misunderstanding of the German text of Weinkauff by these two authors. Weinkauff (1883:27–28) wrote (translated from German): "From Mr. Paetel I received on a loan basis a species, which was labeled *H. corcanica* A. Adams, which, however, could not be separated from *H. discus*, which would be considered a further variety. However, I cannot find where this species is described." Although the second and the third statements contradict one another to a certain extent, my interpretation of the text is that Weinkauff considered the specimen labeled *H. corcanica* A. Adams to be the same as his *H. gigantea* Var. 1 = *H. discus* Reeve, 1846. This particular specimen was not figured by Weinkauff, ruling out the possibility that an illustration could serve the purpose of a valid description. The name is a *nomen nudum*.
69. The type specimen of *H. dubia* Lamarck, 1822, is not in MHNG or the MNHN. Most of Lamarck's types are otherwise deposited in the MHNG (*cf.* Mermod and Binder, 1963).
70. *Haliotis excisa* Gray, 1856, is not listed in Sowerby

(1882) or Weinkauff (1883), but is indicated in Abbott and Dance (1983) and in Pickery (1991) without indication of page number under Gray (1826) and not Gray (1856). *Schismotis excisa* was mentioned in Gray (1856:148), but as a hypothetical name for the teratological specimens with slit tremata he had at hand: "When I first saw the shell, I was inclined to regard it as a monstrosity; but when I considered the uniformity . . . in the specimens . . . , I thought that it might be the type of a new form, for which *Schismotis excisa* would be a good name. . . . I am inclined to believe that the slit in the specimens is . . . caused by the eroded and evidently diseased state of the specimens." Clearly, no new taxa had been described and the genus and species are unavailable.

71. *Haliotis fatui* Rheder [*sic*], 1981, is mentioned in Ubaldi (1993:II 3–1). The date is most likely based on Kaicher's (1981: card no. 2902) statement: "This subspecies [of *H. varia* Linnaeus, 1758] is currently under study by Dr. Harald Rehder (USNM) and will probably be described in detail before the end of the year (1981)." The name was mentioned a second time in the same year (Anon. , 1981). However, the species description was never published. The proposed type specimen for the species from Tonga has been deposited in the USNM. The name *H. fatui* is currently not available.
72. *Haliotis hanleyana* Ancey, 1881, has some affinities with *H. clathrata* Reeve, 1846 (see also notes 24, 25). However, this identification is highly tentative.
73. *Haliotis californiana* Valenciennes, 1831, *H. interrupta* Valenciennes, 1831, and *H. parma* Valenciennes, 1831, were described from "America." The author stated that it was unknown whether the specimens were obtained from the east or west coast. The specimens were 36 mm and larger, making it unlikely that they could have been the small *H. pourtalesii* Dall, 1881, *H. dalli* Henderson, 1915, or *H. roberti* McLean, 1970. *Haliotis parma* has markings from the shell muscle in the shell (Valenciennes, 1831), which additionally suggests that it represents one of the large California species. If *H. californiana*, *H. interrupta*, or *H. parma* should be synonyms of either *H. fulgens* Philippi, 1845, *H. kamtschakana assimilis* Dall 1878, *H. walallensis* Stearns, 1898, or *H. sorenseni* Barsch, 1940, then Valenciennes' name would have priority; the other Californian species (*H. cracherodii*, Leach, 1814, *H. corrugata*, Wood, 1828, *H. rufescens* Swainson, 1822) were described before 1831. *Haliotis interrupta* has been synonymized with *H. cracherodii*, and *H. californiana* with *H. rufescens* (Carpenter, 1864:521 *fide* McLean, 1966:156, 159); the synonymy of *H. parma* is unresolved and the taxon is treated here as a *nomen dubium*. If any of Valenciennes' taxa should eventually be shown to be senior synonyms, then an application to the ICZN for the suppression of Valenciennes' taxa would be advisable.
74. Karsten (1789) published two names for *Haliotis*, *H. iridis* Karsten, 1789, and *H. plicata* Karsten, 1789. These two taxa are synonyms of *H. iris* Gmelin, 1791, and *H. australis* Gmelin, 1791, respectively. Karsten's taxa would be the senior synonyms, but Rosenberg (1996) has formulated a case to suppress Karsten's work that is currently pending with the ICZN. His argument, based on ICZN Article 80, is accepted here.
75. *Haliotis modesta* auct. was mentioned by Menke (1845:194) as a juvenile specimen of *H. capensis* Dunker, 1844 (= *H. midae* Linnaeus, 1758). The original source of *H. modesta* is unknown to me. Menke (1845), as the only author, also put *H. semiplicata* Menke, 1843, into synonymy with *H. capensis*. I do not accept his opinion for the following reasons. *H. semiplicata* occurs exclusively in Australian waters, whereas *H. midae* is endemic to South Africa. Comparisons of the shells of adult *H. semiplicata* and juvenile *H. midae*, which are of the same size, reveal the following characters. *Haliotis semiplicata* has distinct spiral cords, whereas in *H. midae* they are only weakly developed. Spiral undulations form nodes in the middle of the shell of *H. semiplicata*, which give rise to a slight, but fairly distinct, spiral ridge, whereas *H. midae* tends to forms a spiral depression approximately one third from the suture. The shape of *H. semiplicata* is much more elongated than the rotund shell of *H. midae* from a size of approximately 2–3 cm onwards.
76. *Haliotis schroeteri* Menke is mentioned by Weinkauff (1883:83) as a taxon of doubtful status. Weinkauff indicated a potential synononymy with *H. scutulum* Reeve, 1846 (= *H. varia* Linnaeus, 1758 ?, *cf.* note 48). Weinkauff did not know of the original publication, and it is not listed in Sherborn (1922; 1932). I regard it as a *nomen dubium*.
77. A specimen labeled as type of *H. victoriae* Brazier is known from the SAM (R. Pickery, pers. comm.); however, no formal description has been located so far, which renders the name unavailable (ICZN Article 12c). The specimen can be identified as a *H. rubra* Leach, 1814. Any description of *H. victoriae* is very likely to have been published after 1814, as the only abalone species had been described by Brazier in 1878. In case a published description of *H. victoriae* should be found, the taxon would then only become a further junior synonym of *H. rubra*.

VALID SPECIES BY FAUNAL REGIONS:

The broad geographical distribution is indicated below for each taxon considered valid here. In the case of a minor overlap the species is listed only in the major province. The format of the entries is as follows: taxon. + synonyms. (Figures herein). Geographic distribution (illustrations) [Notes]. *Nomina dubia*, *nomina nuda* and unavailable names are not included under the synonymies. Tentative synonyms are indicated by a question

mark after the taxon, and the author of a synonym is only indicated in case of homonymy (see Index to Species-Level Taxa for details).

The distributions of the species are mainly according to Macnae and Kalk (1958), Kira (1962), Habe (1964), McLean (1978), Muller (1984b), Ubaldi (1986), Dharma (1988), Herbert (1990), Wilson (1993), Geiger (1996), Stewart and Geiger (in press), and various collection records in museums and private collections. Species occurring in more than one province are marked with an asterix and are cross-referenced; their distribution is indicated for the area within the respective province.

The list of illustrations is not exhaustive, but focuses on the more recent publications. The following numerical code has been used: 1, Abbott (1954); 2, Kira (1962); 3, Habe (1964); 4, Keen (1971); 5, Hinton (1972); 6, Dance (1974); 7, Hinton (1978); 8, Powell (1979); 9, Eisenberg (1981); 10, Kaicher (1981); 11, Bosch and Bosch (1982); 12, Kilburn and Rippey (1982); 13, Abbott and Dance (1983); 14, Sharabati (1984); 15, Stewart (1984); 16, Wells and Bryce (1985); 17, Springsteen and Leobrera (1986); 18, Richards (1987); 19, Dharma (1988); 20, Drivas and Jay (1988); 21, Salvat *et al.* (1988); 22, Poppe and Goto (1991); 23, Barash and Danin (1992); 24, Wilson (1993); 25, Giannuzzi-Savelli *et al.* (1994); 26, Geiger (1996); 27, Stewart and Geiger (in press); 28, Simone (in press).

Species that have seldom been figured (*H. dissona* (Iredale, 1927), *H. exigua*, *H. jacnensis* Reeve, 1846, *H. marmorata* Linnaeus, 1758, *H. neglecta*, *H. planata*, *H. queketti* Smith, 1914, *H. rubiginosa* Reeve, 1846, *H. speciosa* Reeve, 1846; *H. unilateralis*) are here illustrated in Figures 10–33 along with some noteworthy specimens (*H. diversicolor* Reeve, 1846, from Bali, *H. striata* Linnaeus, 1758).

Caribbean

sp. nov. Simone, in press. Venezuela to central Brazil (28) [note 1].

pourtalesii Dall, 1881 S Florida to Surinam (10, 13) [notes 1, 2, 3].

European and Senegalese

marmorata Linnaeus, 1758. + *decussata*, *guineensis*, *rosacea*, *strigata*, *virginea* Reeve (*non* Gmelin). (Figures 18–19). Central W Africa (10 [as *H. guineensis*], 13 [as *H. rosacea*]) [notes 4, 5, 6, 7].

neglecta Philippi, 1848 (Figures 20–21). Isl. S of Italy [notes 5, 8, 9].

° *pustulata cruenta* Reeve, 1846. Israel and Lybia; see also east African province (10 [as *H. cruenta*], 14, 23, 25) [notes 10, 11, 12].

tuberculata tuberculata Linnaeus, 1758. + *bistriata* Gmelin, *bistriata* Costa, *bisundata*, *incisa*, *janus*, *japonica*, *lamellosa*, *lucida*, *parva* Risso (*non* Linnaeus), *pellucida*, *reticulata*, *rugosa* Reeve (*non* Lamarck), *secernenda*, *striata*, *varia* Risso (*non* Linnaeus), *vulgaris*. Mediterranean, Brittany to Morocco (10 [as *H. lamellosa*], 13, 22) [notes 4, 5, 13, 14 15, 16].

tuberculata coccinea Reeve, 1846. + *canariensis*, *zealandica*. Canary Isl., Azores (10, 22 [both as *H. coccinea*]) [notes 5, 13, 17, 18].

South African

midae Linnaeus, 1758. + *capensis*, *elatior*. St. Helena Bay to W Transkei (6, 10, 12, 13, 18) [note 4].

parva Linnaeus, 1758. + *canaliculata* Fischer ?, *canaliculata* Lamarck, *carinata*, *cingulata*, *kraussi*, *rubicunda* Röding, *rubicunda* (Montfort). False Bay to East London (10, 12, 13, 18) [notes 4, 19, 20].

queketti Smith, 1910 (Figures 24–25). Transkei to S Mozambique (10).

spadicea Donovan, 1808. + *ficiformis*, *sanguinea*, *sinuata* ? Partridge Point, Cape Peninsula to N Natal (9, 10, 12, 13, 18) [notes 21, 22].

speciosa Reeve, 1846. + *alfredensis*. (Figures 30–31). Port Alfred to W Transkei (10 [also as *H. speciosa* form *alfredensis*], 13, 18).

Eastern African, Red Sea and Persian Gulf

° *clathrata* Reeve, 1846. + *venusta*. Kenya, Madagascar, Mascarene Isl., Rodrigues Isl. , Aldabra, Seychelles, Chagos Arch., Maldives; see also tropical Pacific province (5 and 19 [both as *H. crebriculpta*], 10 and 27 [also as *H. venusta*]) [note 24, 25].

mariae mariae Wood, 1828. Oman (10, 11) [note 26].

mariae dentata Jonas, 1846. Oman (10 [as *H. mariae* form *dentata*]) [note 26].

pustulata pustulata Reeve, 1846. + *jousseaumi*. N South Africa to Persian Gulf (10) [notes 10, 11, 12].

° *pustulata cruenta* Reeve, 1846. Particularly Red Sea; see also European and Senegalese province (10 [as *H. cruenta*], 14, 23, 25) [notes 10, 12].

squamosa Gray, 1826. + *roedingi*. S Madagascar (15, 27) [notes 27, 28, 29].

unilateralis Lamarck, 1822 (Figures 32–33). Central E Africa to Red Sea, Aldabra, Madagascar, Mascarene Isl. (14 [as *Sanhaliotis pustulata*], 20 [as *H. varia*], 26) [note 30].

rugosa Lamarck, 1822. + *alternata*, *multiperforata*, *nebulata*, *pertusa*, *revelata*. Mascarene Isl., Madagascar, central E Africa (6 and 20 [both as *H. pustulata*], 10 [as *H. pustulata* form *alternata*]) [notes 11, 31, 32, 33].

Indian Ocean and Tropical West Pacific

asinina Linnaeus, 1758. + *asinum*. S-most Japan to Sydney, Andaman Isl. to New Caledonia (2, 5, 6, 7, 10 [juvenile and adult], 13 16, 17, 19, 24) [note 4].

brazieri Angas, 1869. + *melculus*. (Figures 4–5). S Queensland to Jervis Bay, New South Wales (7, 10, 13, 24) [notes 34, 35].

° *clathrata* Reeve, 1846. + *venusta*. Andamans to American Samoa, S Japan to Sydney; see also east African province (5 and 19 [both as *H. crebriculpta*], 10 and 27 [also as *H. venusta*]) [note 24, 25].

crebriculpta Sowerby, 1914. New Caledonia (10, 27) [notes 25, 36].

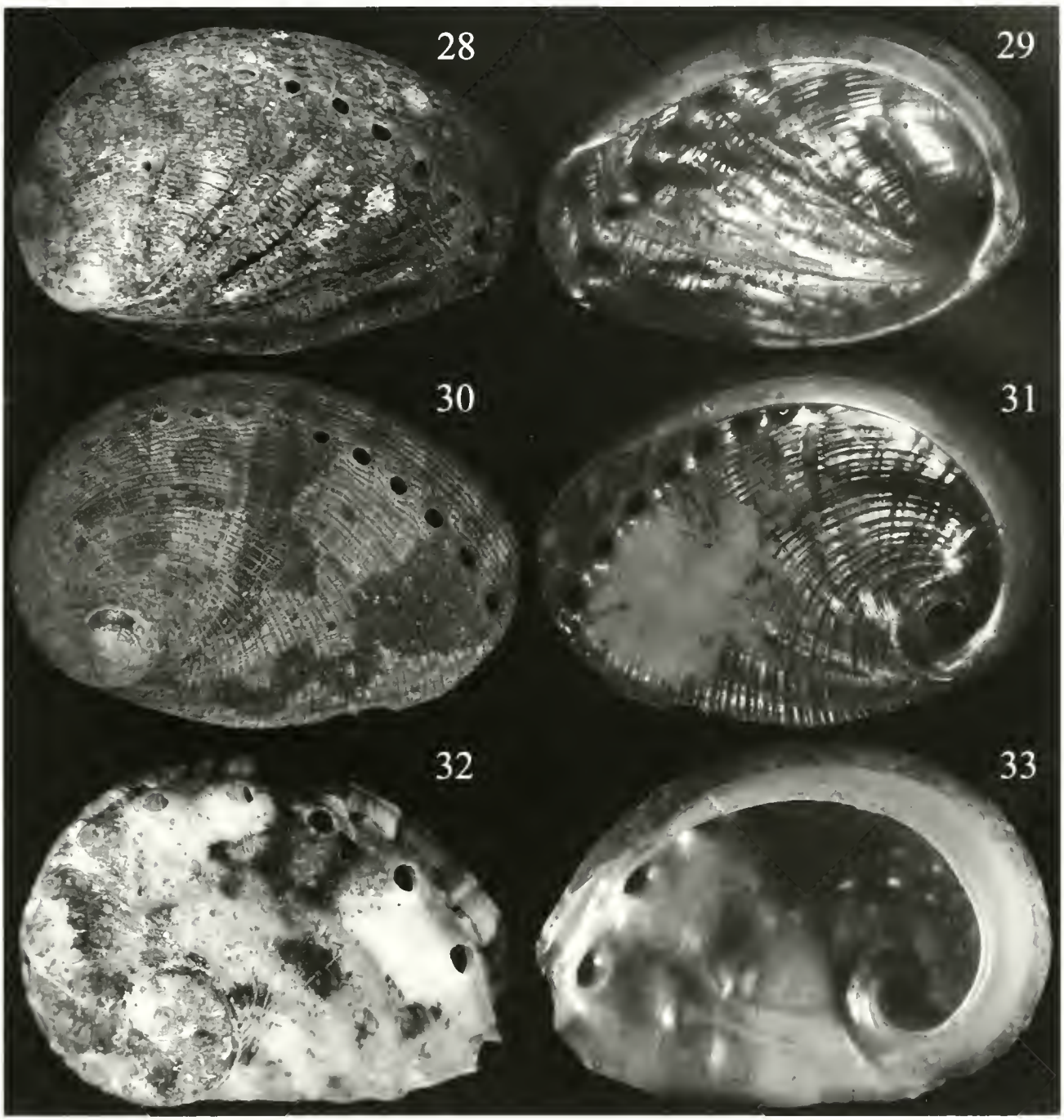
° *diversicolor* Reeve, 1846. + *aquatilis*, *gruneri*, *supertexta*, *tayloriana*. (Figures 12–13). China, Taiwan, Bali; see also northwestern Pacific province (2 [as *H. supertexta*], 3, 10 [also as forms *gruneri*, *tayloriana*, *supratexta*, and *H. aquatilis*]) [notes 37, 38].

dissona (Iredale, 1929). (Figures 10–11). Queensland, New Caledonia, Tonga (10) [note 36, 39].

dohrniana Dunker, 1863. New Caledonia, Tonga (10, 21, 27) [note 40].

glabra Gmelin, 1791. + *picta*, *ziczac*. Philippines, Maluku, Lesser Sunda Isl. (9, 10, 13, 17, 19 [as *H. planata*]).

hargravesi Cox, 1869. + *ethologus*. S Queensland to N New



Figures 28–33. Infrequently illustrated *Haliotis*. **28–29.** *Haliotis striata* Linnaeus, 1758. 56 mm. One of the six specimens in LSL. *Mare europaeus*. **30–31.** *H. speciosa* Reeve, 1846. 31 mm. NMW 1955. 158. 2126. Algoa Bay. **32–33.** *H. unilateralis* Lamarck, 1822. **32.** 23mm. Collection S. Singer. Red Sea, Gulf of Aquaba, **33.** 24 mm. Collection Geiger AAB 48a. Elat, Red Sea.

South Wales (7, 13, 10 and 24 [both also as *H. ethologus*]) [notes 34, 35].

jacnensis Reeve, 1846. + *echinata, hanleyi*. (Figures 16–17). S-most Japan (S of Amami Isl.), Philippines, New Caledonia, Marianas, Micronesia (3, 10 [also as *H. hanleyi*]) [notes 31, 41].

ovina Gmelin, 1791. + *caelata, latilabris*. Maldives to Tuamotus, SW Japan, Philippines, Vietnam, Queensland to Western Australia (2, 5, 7, 9, 13, 16, 17, 19, 21, 24) [note 8].

° *planata* Sowerby, 1882. + *grayana*. (Figures 22–23). Philippines to Fiji, Northern Territories; see also northwestern Pacific province (10 [also as *H. grayana*]) [notes 31, 42].

pulcherrima Gmelin, 1791: Tuamotus, Henderson Isl. (9, 10, 13).

rubiginosa Reeve, 1846. + *howensis*. (Figures 26–27). Lord

Howe Isl. (10 [as *H. varia rubiginosa* and *H. howensis*], 7 and 13 [both as *H. howensis*]) [note 43].

varia Linnaeus, 1758. + *aliena, astricta, barbouri, concinna, dringii, gemma, granulata, papulata, pustulifera, scutulum, semistriata, viridis.* Sri Lanka to Tonga, S Japan, Philippines, central W Western Australia to Sydney (2, 5, 7, 9, 10 [also as ssp. *astricta, papulata, pustulifera, viridis,* and *H. unilateralis*], 13, 16, 19) [notes 1, 4, 44, 45, 46, 47, 48].

Temperate Australian

coccoradiata Reeve, 1846. New South Wales to E Victoria (7, 9, 10, 24) [note 49].

cyclobates Péron, 1816. + *excavata.* South Australia to central S Western Australia (9, 10 [also as *H. ovina*], 13, 16, 24).

elegans Philippi, 1844. + *clathrata* Lichtenstein (*non* Reeve). Western Australia (7, 9, 10, 13, 16, 24) [notes 23, 50].

laevigata Donovan, 1808. + *albicans, glabra* Swainson? (*non* Gmelin). Victoria to SW Western Australia (6, 7, 10, 13 16, 24).

roei Gray, 1826. + *scabricostata, sulcosa.* Victoria to central W Western Australia (6, 7, 10 [also as *H. sulcosa*], 13, 16, 24) [note 27].

rubra rubra Leach, 1814. + *ancile, improbula, naevosa, whitehousei.* New South Wales to South Australia, Tasmania (7 and 13 [both as *H. ruber*], 10 [also as *ruber, r. improbulum, ancile*]) [notes 25, 27, 51, 52, 53, 54, 55].

rubra conicopora Péron, 1816. + *cunninghami, granti, vixlirata.* Victoria to Freemantle SW Western Australia. (7, 16, 24 [all as *H. conicopora*], 10 [also as *H. c. vixlirata*]) [note 53].

scalaris scalaris (Leach, 1814). + *crenata* ?, *tricostalis, tricostata.* W South Australia to central W Western Australia (7, 9, 10, 13, 16, 24) [notes 24, 56].

scalaris emmae Reeve, 1846. Victoria to W South Australia (7, 10, 13, 24 [all as *emmae*]) [note 56].

semiplicata Menke, 1843. + *lauta.* SW Western Australia (7, 13, 24) [note 49].

squamata Reeve, 1846. + *elevata, funebris, stomatiaeformis.* Central W Western Australia to Northern Territories, Bali (7, 9, 10, 16, 19, 24) [notes 31, 39, 57, 58].

New Zealand

australis Gmelin, 1791. + *aleata, costata, rugosoplicata.* New Zealand (8, 10, 13) [note 59].

iris Gmelin, 1791. New Zealand (6, 8, 10, 13) [note 54].

virginea virginea Gmelin, 1791. + *gibba, marmorata* Reeve (*non* Linnaeus), *subvirginea.* S South Isl. and Stewart Isl., N South Isl. to S North Isl. (6, 8, 10) [notes 60, 61].

virginea crispata Gould, 1847. NE North Isl. (8, 10) [note 60].

virginea huttoni Filhol, 1880. Auckland Isl., Chapman Isl. (8, 10) [note 60].

virginea morioria Powell, 1938. Chatham Isl. (8, 10) [note 60].

Northwestern Pacific

° *diversicolor* Reeve, 1846. + *aquatilis, gruneri, supertexta, tayloriana.* (Figures 12–13). S Hokkaido; see also tropical Pacific province (2 [as *H. supertexta*], 3, 10 [also as forms *gruneri, tayloriana, supratexta,* and *H. aquatilis*]) [notes 37, 38].

discus discus Reeve, 1846. Honshu, Kyushu, Shikoku (10) [note 62].

discus hannai Ino, 1953. Korea, Hokkaido, NE Honshu (2, 10, 13) [note 62].

exigua Dunker, 1877 (Figures 14–15). S Japan (Okinawa) (10) [note 63].

gigantea Gmelin, 1791. + *gigas, sieboldii, tubifera.* Honshu (2, 10) [note 64].

madaka (Habe, 1977). S and central Honshu, Kyushu (2, 10 [both as *sieboldii*]) [note 64].

° *planata* Sowerby, 1882. + *grayana.* (Figures 22–23). S of Yakushima; see also tropical Pacific province (10 [also as *H. grayana*]) [notes 31, 42].

Northeastern Pacific

cornugata Wood, 1828. + *diegoensis, nodosa, oweni.* Central to central Baja California (1, 6, 9, 10 [also as ssp. *oweni*], 13) [notes 26, 65, 66].

cracherodii Leach, 1814. + *bonita, californiensis, expansa, holzneri, imperforata* Dall (*non* Gmelin), *lusus, rosea, splendidula.* N California to central Baja California (1, 6, 9, 10 [as *H. cracherodii californiensis* and *H. c. cracherodii*], 13) [note 66].

fulgens Philippi, 1845. + *guadalupensis, planilirata, splendens, turveri.* Central California to central Baja California (1, 6, 10 [also as ssp. *guadalupensis*], 13) [note 47].

kamtschatkana kamtschatkana Jonas, 1845. Alaska to Point Conception, S California (1, 10, 13) [notes 62, 67].

kamtschatkana assimilis Dall, 1878. + *aulaea, smithsoni.* Central to S California (1, 9, 10, 13 [all as *H. assimilis*]) [notes 62, 67].

rufescens Swainson, 1822. + *californiana, hattorii, ponderosa.* N California to Central Baja California (1, 6, 13).

sorenseni Bartsch, 1940. Point Conception to central Baja California (10).

walallensis Stearns, 1898. S Washington to S California (10, 13).

Tropical Eastern Pacific

dalli Henderson, 1915. Galapagos Isl., Gorgona Isl. (4, 10, 13) [note 2].

roberti McLean, 1970. Cocos Isl. (4, 10) [note 2].

ZOOGEOGRAPHY:

The species in South Africa, New Zealand and the northeastern Pacific are all endemic, and with the exception of one questionable report (Macpherson, 1953: the South African *H. spadicea* Donovan, 1808, in Australia) no wide spread species have been found in these areas. The East African and the Indo-Pacific provinces are also more or less isolated from each other; Geiger (1996) discussed the apparent faunal barrier around India. Only *H. clathrata* Reeve, 1846, occurs in both areas (Stewart and Geiger, in press). Indications particularly of *H. varia* in the East African province, and *H. pustulata* in the central Indo-Pacific are erroneous (Geiger, 1996; pers. obs.). In the Australian province the separation of tropical and temperate species is not very sharp; considerable overlap has to be noted for a few species. Only a limited number of species are widespread over several faunal provinces, *i.e., H. asinina, H. clathrata* Reeve, *H. ovina* and *H. varia.* A much more detailed, specimen based account of the distribution of all abalone species will be provided elsewhere.

Three biogeographical models have been introduced and are reviewed in Geiger and Groves (submitted). Talmadge (1963a) proposed the Pacific Rim hypothesis with multiple centers of radiations along the Pacific islands

from Japan to Australia and New Zealand. Lindberg (1992) pointed to the highest diversity of abalones being found in the central Indo-Pacific, which may (or may not) indicate the origin of the group there. Based on published chromosomal data Geiger and Groves (submitted) suggested a potential origin of abalone in the Tethys Sea, which is also discussed by Lee and Vacquier (1995).

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On the Identity of *Buccinum labyrinthus* Gmelin, 1791 (Gastropoda: Buccinidae) from the Netherlands Coast

Guido Pastorino
Depto. Paleozoología Invertebrados
Museo de La Plata
Paseo del Bosque s/n
1900 La Plata, Buenos Aires
ARGENTINA
rvpastor@criba.edu.ar

Yuri Kantor
A.N. Severtzov Institute of Problems of Evolution
Russian Academy of Sciences
Lenmskij Prospect, 33
Moscow 117071 RUSSIA
yuri@invert.sevin.msk.ru

Buccinum labyrinthus was described and illustrated by Martini (1777, Vol. 3, Pl. 120, fig. 1103) who based the new taxon on a single specimen from Scheweningen, Holland. Martini's work, however, was rejected for nomenclatorial purposes by the International Commission on Zoological Nomenclature (1954). Gmelin (1791), having cited both the name and Martini's illustration, is considered to be the author of *B. labyrinthus*. The specimen illustrated by Martini, deposited at the Zoologisk Museum, Kobenhavns Universitet, Denmark (ZMUC), is the holotype of *B. labyrinthus*.

In his monograph of the family Nassidae, Tryon (1882) listed *Buccinum labyrinthus* as a probable senior synonym for *Buccinanops cochlidium* Chemnitz (= *Buccinanops cochlidium* (Dillwyn, 1817)) from the Patagonian coast, calling into question the Dutch type locality. In a revision of the *Bullia* group, Allmon (1990) followed Tryon in reporting *B. labyrinthus* as a possible older name for *Buccinanops cochlidium*.

In the course of preparing revisions of several families of southern South American gastropods, the senior author has had the opportunity to examine the type material of many Patagonian species housed in European museums, and to compare these types with fresh-collected material. Examination of the type of *Buccinum labyrinthus* revealed that it was neither conspecific nor congeneric with *Buccinanops cochlidium*, but more likely represented a grossly deformed specimen of a common local species.

The John Gwyn Jeffreys Collection, housed in the National Museum of Natural History, Smithsonian Institution, since the 1880s (Warén, 1980), contains a large number of teratological specimens of common European species, among them several severely deformed *Buccinum undatum* from England. Comparisons of the holotype of *Buccinum labyrinthus* Gmelin with some of the specimens from Jeffrey's Collection revealed striking similarities in shell shape (Figs. 1–8). Such deformities are likely a result of trauma to the mantle edge and the outer lip of the shell by a predator. The adapical regions of the spires resemble those of undamaged specimens of *Buccinum undatum*, while the onset of abnormal morphology is demarcated by an obvious, repaired break in the shell.

The holotype of *Buccinum labyrinthus* has such a shell scar on the upper portion of its spire (Fig. 3, arrow), after which the distortion of the whorls begun and the characteristic shoulder cord was formed.

The originally reported type locality of *Buccinum labyrinthus* falls within the geographic range of *Buccinum undatum*, which extends from Labrador to the eastern Barents Sea (Golikov, 1980) and is close to the area where the deformed Jeffreys' specimens were collected.

We therefore place *Buccinum labyrinthus* Gmelin, 1791 in the synonymy of *Buccinum undatum* Linnaeus, 1758. *Buccinum labyrinthus* is not a senior synonym of *Buccinanops cochlidium* (Dillwyn, 1817), as suggested by Tryon (1882) and Allmon (1990).

ACKNOWLEDGMENTS

Special thanks are due to Tom Schiotte, Zoologisk Museum, Kobenhavns Universitet, who kindly provided photographs of the type of *Buccinum labyrinthus*, and to M. G. Harasewych, National Museum of Natural History, Smithsonian Institution, for his hospitality during our work at the USNM.

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Figures 1–8. *Buccinum undatum* Linnaeus, 1758. **1–3.** Holotype of *Buccinum labyrinthus* Gmelin, 1791, ZMUC unnumbered, Scheweningen, Holland, length 56 mm. **4–5.** USNM 191932, Jeffreys collection, Whistables Flats, England, length 59 mm. **6–7.** USNM 192081, Jeffreys Collection, no locality data, length 64.2 mm. **8.** USNM 192082, Jeffreys Collection, no locality data, length 56.3 mm. Arrows indicate repaired break and onset of deformity.

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JUN 04 1998

Eight Aporrhaid Gastropod Species from the Cretaceous of the Pacific Slope of North America and Clarification of the Type Species of *Perissoptera*

L. R. Saul
Natural History Museum of Los Angeles County
900 Exposition Boulevard
Los Angeles, CA 90007 USA
lulasaul@aol.com

ABSTRACT

Eight aporrhaid species from Pacific Slope deposits of late Early Cretaceous through early Late Cretaceous age are assigned among three genera, *Aporrhais*, *Latiala*, and *Alarimella* n. gen. Except for two species of *Latiala*, *Latiala* sp. of Albian age from Oregon and *Latiala heliaca* n. sp. of Cenomanian age from Fresno and Shasta counties, California, the species are of Turonian age. Pacific Slope *Latiala* was most species-diverse during the Turonian and has not been found in younger Pacific Slope deposits. The three Turonian *Latiala* are *Latiala californica* (Gabb) from Siskiyou and Shasta counties, California, *Latiala sigma* n. sp. from the Redding area, Shasta County, and *"Alaria" nodosa* Packard, 1922, from the the Redding area, Shasta County, and the Santa Ana Mountains, Orange County, California. *Aporrhais drachuki* n. sp. is from the Santa Ana Mountains, as are two species included in *Alarimella* n. gen., *Alarimella anae* n. sp. and the reassigned species, *Alarimella vetus* (Packard, 1922). *Alarimella* resembles *Rimella* of the Strombidae, but possesses an expanded outer lip. The total number of Turonian aporrhaids known from the Santa Ana Mountains, southern California is increased to six species and includes the first record of *Aporrhais* on the Pacific Coast of North America. Selection of a type species for *Perissoptera* from among Cretaceous species listed by Tate, 1865 ensures that *Arrhoges* is not supplanted by *Perissoptera*.

Key words: Aporrhaidae, *Aporrhais*, *Perissoptera*, *Latiala*, *Alarimella*, Cretaceous, Turonian, California.

INTRODUCTION

This paper adds two new species to the four species of Aporrhaidae previously recorded from beds of Turonian age in the Santa Ana Mountains, Orange County, California. *Anchura (Helicaulax?) tricosa* Saul and Popenoe, 1993; *Pyktes diaphron* Popenoe, 1983; *Alaria nodosa* Packard, 1922 which was considered to be a synonym of *Arrhoges (Latiala) californicus* (Gabb, 1864) by Popenoe, 1983; and *Aporrhais vetus* Packard, 1922, which is, herein, assigned to the new genus *Alarimella*, are the previously described species. The new species are *Aporrhais drachuki* and *Alarimella anae*. Recognition of these species in the Turonian of the Santa Ana Mountains increases the known diversity of aporrhaiids in those faunas and enlarges the paleogeographic distribution of *Aporrhais* to include the West Coast of North America during the Turonian.

Re-examination of *"Alaria" nodosa* and *Latiala californica* indicates that the larger, thicker shelled *"Alaria" nodosa* has fewer axial ribs on the spire and should not be included in *L. californica*. *Latiala californica* is not recognized from the Santa Ana Mountains but is present in the Siskiyou Mountains of Oregon and California and in the Redding area, Shasta County, California. *Latiala nodosa* (Packard, 1922) is a common to abundant fossil in the Turonian of the Santa Ana Mountains and also is present in beds of similar age in the Redding area, Shasta County, California. The third *Latiala* species, *L. sigma* n. sp. is described from the Turonian of the Redding area, Shasta County. A fourth species, *L. heliaca* n. sp., is based upon specimens of Cenomanian age from Sunflower Valley, Fresno County, and specimens formerly identified as *Arrhoges californicus* from the Ono area, Shasta County, California. A fifth species of *Latiala* is recognized from specimens of Albian age from Grave Creek, Jackson County, Oregon. Naming of this new species awaits better preserved material. Table 1 lists the discussed species by age and indicates their geographic distribution. Areas from which these eight species of aporrhaids have been collected are indicated on Figure 1.

Several recent papers have added to the number of aporrhaids described from the Cretaceous of the Pacific Slope. Popenoe (1983) defined the genus *Pyktes* and discussed species ranging in age from Turonian to Maastrichtian. Saul and Popenoe (1993) discussed two species of *Anchura (Helicaulax)* of Turonian age. Elder and Saul (1996) discussed 10 species of *Anchura* with ranges of 1.5 to 4 m.y. within the Late Cretaceous (Coniacian through Maastrichtian interval).

Popenoe (1983) proposed two subfamilies of Apor-

Table 1. Age and geographic distribution of discussed aporrhaid species.

Age	Species	California			Oregon
		S	C	N	
Turonian	*Alarimella anae* n. sp.	X			
	Alarimella veta (Packard, 1922)	X			
	Aporrhais drachuki n. sp.	X			
	Latiala californica (Gabb, 1864)		?	X	X
	Latiala nodosa (Packard, 1922)	X	?	X	
	Latiala sigma n. sp.			X	
Cenomanian	*Latiala heliaca* n. sp.		X	X	
Albian	*Latiala heliaca* n. sp			X	
	Latiala sp.				X

S = southern; C = central; N = northern. Juveniles at various horizons in the Great Valley Sequence on west side of the Great Valley, central California, resemble those of *L. californica*, *L. nodosa*, and *L. heliaca*.

rhaidae, Aporrhainae and Arrhoginae. Among characteristics of Aporrhainae mentioned by Popenoe are a prominent bent digitation on the wing at the shoulder, the digitation bent medially with its distal end posteriorly directed, additional labral digitations developed in some genera, and labral sinuses well developed. Characteristics of Arrhoginae include predominently axially directed sculpture, wing with an entire margin except for a prominent posteriorly directed digitation arising from the posteriolateral border of the outer lip, and, commonly, a straighter rostrum. *Aporrhais drachuki* exhibits characteristics of Aporrhaiinae. *Latiala* sp., *Latiala heliaca, L. californica, L. sigma,* and *L. nodosa* exhibit characteristics of Arrhoginae. Zinsmeister and Griffin (1995 added the subfamily Struthiopterinae for aporrhaids from the southern rim (Weddellian Province) of the Pacific Ocean. Roy (1994) suggested that *Struthioptera* might be an *Arrhoges* Gabb, 1868, but *Struthioptera* and other Struthiopterinae have two spiral carinae and *Arrhoges* lacks carinae. Roy (1994) used 25 morphologic characteristics and divided the Aporrhaiidae into two groups of genera, M1 with multidigitate apertural margins and M2 with simpler apertural margins. He includes *Aporrhais* in M1, and *Arrhoges*, of which *Latiala* Sohl, 1960, was proposed as a subgenus, is in M2.

Alarimella does not fit readily into the above subfamilies. Its elongate shape, short anterior rostrum, posterior canal extending up the spire, and its sculpture resemble those of *Rimella* and other *Rimella*-like gastropods (Clark and Palmer, 1923). *Alarimella* also resembles *Calyptraphorus binodiferus* Perrilliat and Vega, 1997, in its sculpture, but it lacks the callus coating and curled over posterior canal of *C. binodiferus* and has an expanded outer lip shaped somewhat like that of *Drepanocheilus*. The *Rimella*-like gastropods and *Calyptraphorus* are usually classed in the Strombidae from which *Alarimella* differs in having an alately expanded, internally channeled outer lip. *Alarimella* also lacks a strombid notch which perhaps suggests that its eyes were on bulbs at the base of the tentacles as in apporhaids rather than stalked as in strombids.

Temperature implications of the three genera, *Aporrhais, Latiala,* and *Alarimella,* are somewhat equivocal. Undoubtedly the climate of the Santa Ana Mountains during the Turonian was warm; rare rudist fragments are found associated with some of these aporrhaids. Modern *Aporrhais* spp., however, occur from the Baltic to North Africa, and modern *Arrhoges occidentalis,* arguably the closest living relative of *Latiala,* inhabits cool temperate waters from Newfoundland to North Carolina. As Cretaceous aporrhaids were much more widely distributed than are the modern ones, modern *Aporrhais* and *Arrhoges* may not appropriately model the climate for Cretaceous or early Tertiary species. *Latiala* is present in Japan in the Early Cretaceous, Pondoland, India, and the Gulf Coast during the latter part of the Cretaceous, and the Pacific Slope during the mid-Cretaceous, all in associations suggestive of warm water. *Rimella*-like gastropods are tropical to subtropical, and if *Alarimella* is related to them, it may indicate warm waters. The absence of *Latiala* in Pacific Slope post-Turonian deposits coincides with the absence of several other thermophilic molluses (*e.g., Trigonarca, Authonya,* and actaeonellid gastropods) that had been present in the mid-Cretaceous.

Table 1 contrasts some characteristics of the species discussed in this paper. The wing dimensions are described as tall to short in the axial direction (=height) and broad to narrow in the spiral direction (= breadth).

Institutional abbreviations used in this paper are: ANSP, Academy of Natural Sciences of Philadelphia; CASG, California Academy of Sciences, Geology; CIT, California Institute of Technology; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology; UCBMP, University of California, Berkeley, Museum of Paleontology; UCLA, University of California, Los Angeles; USGS, United States Geological Survey; USNM, United States National Museum. Collections of California Institute of Technology and University of California, Los Angeles are at the Natural History Museum of Los Angeles County.

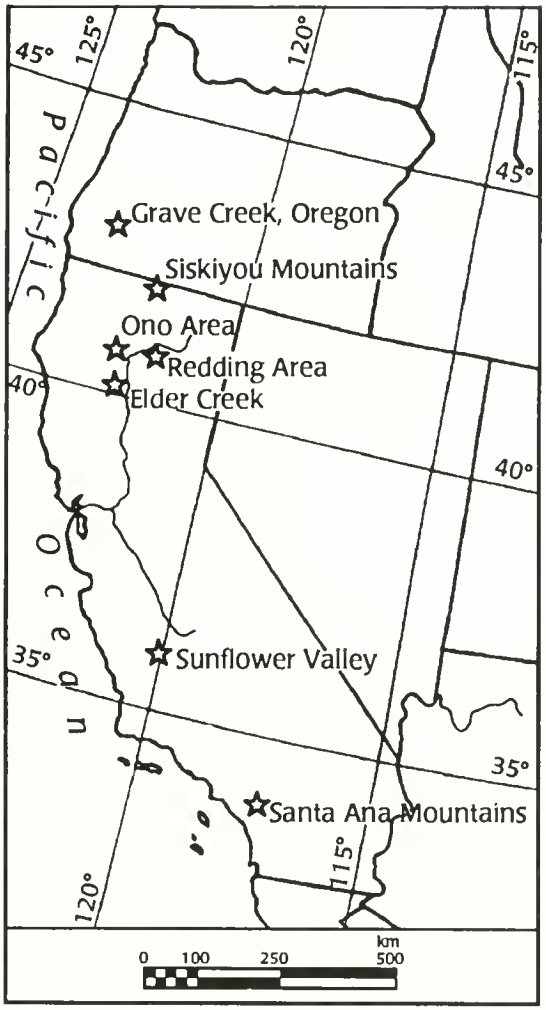


Figure 1. Index map to areas from which eight aporrhaiid species have been collected. **Grave Creek,** Jackson County, Oregon: ?Hornbrook Formation, late early-middle Albian. **Siskiyou Mountains,** Jackson County, Oregon and Siskiyou County, California: Osburger Gulch Sandstone Member of the Hornbrook Formation, Turonian. **Redding area,** Shasta County, California: Frazier Silt and Melton Sandstone Member, Redding Formation, Turonian. **Ono area,** Shasta County, California: Bald Hills Member, Budden Canyon Formation, Cenomanian. **Elder Creek,** Tehama County, California: fossiliferous boulder of Cenomanian or late Albian age in conglomerate of Turonian age. **Sunflower Valley,** Kings County, California: Panoche Formation, Cenomanian. **Santa Ana Mountains,** Orange County, California: Baker Canyon Sandstone and lower Holz Shale Members of Ladd Formation, Turonian.

SYSTEMATIC PALEONTOLOGY

Family Aporrhaidae Gray, 1850
Genus *Aporrhais* da Costa, 1778

Type species: *Aporrhais pespelicani* (Linnaeus, 1758), Recent, European seas.

Discussion: Aporrhais is a medium sized aporrhaid with a palmately expanded wing that has at least three digitations. The digitations are more or less spikey, short to long, and channeled interiorly. The posterior digitation may be very short and entirely adnate to the spire or longer and free for most of its length. The labral digitations of which there are at least two, vary both in number and length even within a species. Each digitation prolongs a cord from the last whorl. The protoconch is multispiral with globose, smooth whorls. The earliest sculpture is of fine spiral cordlets which are soon crossed by fine curved axial riblets. The riblets become stronger and commonly fewer and each develops a node medially. The row of nodes forms the whorl shoulder and commonly coincides with a strong cord as in *Aporrhais uttingeriana* (Risso, 1826). The whorl is subangulate, at least at the shoulder and basally, the more anterior angulation is also noded and/or cordate. The whorl profile between the angulations is commonly concave. At least one additional noticeable cord is commonly present anterior to the anterior angulation. It usually produces a digation in some species, rarely in others. The rostrum is commonly bent, adaperaturally in some species, abaperturally in others and extended by a rostral digitation.

Aporrhais drachuki n. sp.
Figures 2–7; Table 3.

Diagnosis: An *Aporrhais* with two, nearly equal, strong, raised and noded primary cords on the body whorl, and a third somewhat weaker one on the base. Posterior-most cord forming carina on spire whorls.

Description: Shell average sized for *Aporrhais*, moderately high spired, pleural angle about 44°; about six post-nuclear whorls, angulate near mid whorl on spire, biangulate on body whorl; suture impressed; protoconch unknown; varices randomly present on early whorls; growth line antispirally concave on spire. Juvenile sculpture of fine collabral ribs; adolescent sculpture of about 20 rounded arcuate ribs, strongly noded at the mid whorl angulation; ribs greatly reduced on body whorl but producing strong nodes on posterior and anterior angulation; three nearly equidistant spiral cords on body whorl, strongest on posterior angulation and weakest anterior to anterior angulation; surface of body whorl covered by fine raised spirals, about three per mm, becoming stronger and fanning out onto wing; posterior and middle cords (primary cords) forming two angulations and digitations on wing. Outer lip expanded palmately to form wing. Inner lip with finger of callus extending adapically beyond the first suture, callus broad and rather thin parietally, thicker and with more defined edge at basal sulcus. Rostrum moderately short and narrow.

Type specimens: Holotype LACMIP 11373; paratypes LACMIP 11375 and 11376 from CIT loc. 1058 (=LACMIP loc. 10890), LACMIP 11374 from CIT loc. 1065 (=LACMIP loc. 10891), LACMIP 11377 from CIT 1064 (=LACMIP loc. 10893).

Type locality: LACMIP loc. 15295, south side of Sil-

Table 2. Some characteristics of discussed aporrhaid species. Measurements and ratios are averages from Tables 3–10.

	Posterior canal	Wing shape	WH/WB	A	Dp/Hp	R	Rj	C
Aporrhais drachuki n. sp	?	palmate	1.52 ± 0.26	41° ± 4.8	1.7 ± 0.2	10	24	3
Latiala n. sp.	no	quadrate	0.94 ± 0.1	30° ± 1.5	1.6 ± 0.2	8	20	0
L. heliaca n. sp	no	quadrate	0.90 ± 0.05	36° ± 3.2	2.0 ± 0.3	3–	28	0
L. californica (Gabb)	no	quadrate	0.76 ± 0.06	35° ± 4.0	1.9 ± 0.2	4–	40	0
L. sigma n. sp.	no	quadrate	0.83 ± 0.06	35° ± 3.2	1.8 ± 0.2	7	52	0
L. nodosa (Packard)	no	quadrate	1.12 ± 0.20	36° ± 4.2	1.0 ± 0.1	7	20	0
Alarinella anae n. sp.	yes	pointed	0.44	31° ± 2.3	1.8 ± 0.1	0?	14	0
A. veta (Packard)	yes	triangular	0.73 ± 0.15	26° ± 2.8	1.8 ± 0.2	14	?	

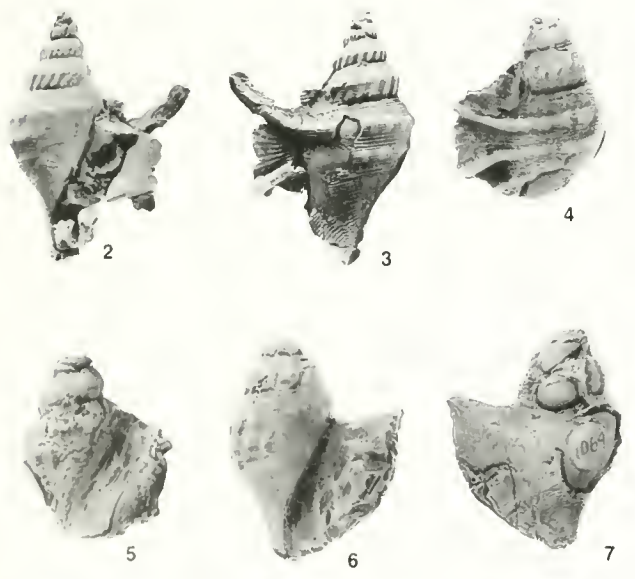
A = pleural angle; C = number of cords on body whorl; Dp/Hp = ratio of whorl diameter to whorl height; R = number of axial ribs on body whorl; – = ribs present only on back of whorl; Rj = number of axial ribs on juvenile whorl; WH/WB = ratio of wing height to wing breadth.

verado Canyon, 1025'N, 150'E of SW cor. sec.8, T5S, R7W, El Toro quadrangle, Santa Ana Mts., Orange County, California. Ladd Formation, top of Baker Canyon Sandstone Member; Turonian.

Dimensions: See Table 3.

Age: Late Turonian.

Geographic distribution: Known only from the Ladd Formation, Baker Canyon Sandstone and lower Holz Shale Members, Santa Ana Mountains, Orange County, California. (LACMIP loc. 15295, 1 spec; CIT loc. 1064, 1 spec.; LACMIP loc. 10898, 2 spec.; CIT loc. 1058, 3 spec.; CIT loc. 454, 1 spec.; CIT loc. 1065, 1 spec.; LACMIP loc. 10955, 2 spec.).



Figures 2–7. *Aporrhais drachuki* n. sp., all ×1 and whitened with ammonium chloride. **2–3.** Holotype LACMIP 11373 from LACMIP loc. 15295, **2,** aperture, **3,** back view. **4–5.** Paratype LACMIP 11375 from CIT 1058, **4,** back view, **5,** aperture. **6–7.** Paratype LACMIP 11377, from CIT 1064, **6,** aperture, **7,** back view.

Remarks: *Aporrhais drachuki* may be the earliest described *Aporrhais*. Wenz (1940) listed *Aporrhais* as Senonian (Europe) to Recent (Europe), but Roy (1994) depicts it as being present in the Cenomanian. Sohl (1967) reviewed North American species ascribed to *Aporrhais*. He concluded that *Aporrhais biangulata* (Meek and Hayden, 1856) of Maastrichtian age from the upper part of the Pierre Shale of Wyoming and Montana and an undescribed species of early Campanian age from the Blufftown Formation of Alabama were the only actual *Aporrhais* from the Cretaceous of North America known to him. Kase (*in* Kase and Maeda, 1980) described *Perissoptera elegans* Kase, 1980, of Barremian age, a species with an anterior digitation that is more spiky than lobate and not typical of *Perissoptera* Tate, 1865. The spiky labral digitations are suggestive of *Aporrhais*, but *P. elegans* appears to have no posterior digitation adnate to the spire. *Perissoptera elegans* is considerably earlier than *Aporrhais drachuki* and has characteristics that may be intermediate between *Drepanochilus* and *Aporrhais*. *Aporrhais drachuki* differs from *A. biangulata* in having stronger nodes on its two prominent spiral cords, a more angulate whorl profile to the spire, and better developed axial ribs. In having a well noded adapical cord and noticeable third cord, *Aporrhais drachuki* is more similar to *A. pespelecani* than is *A. biangulata*. The primary spiral cords of *A. drachuki* are relatively stronger and the nodes on them less prominent; the two primary cords are more nearly equal (the posterior cord is only slightly stronger); and indications are for a posterior apertural digitaion that is much shorter than in *A. pespelecani*. The over all shape and sculpture pattern are very similar. The posterior edge of the outer lip in *A. drachuki* has a well developed posterior sinus that causes the lip edge to bend backward between the posterior adnate digitation and apparent posterior labral digitation. A complete distal edge to the wing is not preserved in any available specimen of *A. drachuki*. None of the specimens preserves a digitation adnate to the spire. Paratypes have extensions of callus adapically from the posterior end of the aperture that may be remnants of an adnate posterior digitation.

Table 3. Measurements in mm of specimens of *Aporrhais drachuki* n. sp.

	H	Hp	D	Dp	Dp/Hp	S	A	R	Rj	Rp	WB	WH	WD	Whorls
LACMIP 11373	35.0	5.9	13.4	10.0	1.7	14.0†	47°	10	24	20	8.0†	12.5†	17.0	6
LACMIP 11374	17.6†	4.0	7.7	5.5	1.4	10.7†	34°	—	—	—	5.0	8.4	11.0	6
LACMIP 11376	20.8†	5.2	12.0†	9.0	1.7	—	44°	—	—	—	—	—	—	3+
LACMIP 11375	23.8†	5.5	14.5†	9.7	1.8	—	42°	—	—	—	9.6	16.0†	—	3
LACMIP 11377	29.9†	5.5	14.0	10.5	1.9	13.0†	42°	—	—	16•	13.0	14.8	19.6†	4

A = pleural angle; D = diameter last whorl; Dp = diameter of penultimate whorl; H = height; Hp = height penultimate whorl; R = axial ribs on body whorl; Rj = axial ribs on juvenile whorl; Rp = axial ribs on penultimate or other late teleoconch whorl; S = height of spire; WB = wing breadth measured from last rib to distal edge; WD = length distal margin of wing; WH = wing height except posterior and anterior spurs; † = broken, crushed; • = axial ribs counted on one side of whorl and doubled.

Roy (1994) suggests that in *Aporrhais* of Cretaceous age, the apertures are less heavily callused than in *A. pespelecani*. The holotype of *A. drachuki* is only lightly callused about the aperture, but it may not have been sufficiently mature to have developed a complete callus deposit. Paratype 11375 has a thicker callus deposit on the inside of the outer lip, but it, too, is not as thick as that of *A. pespelecani*.

Etymology: The species is named for Robert Drachuk, an amateur collector, who found the holotype of this species and donated it to W. P. Popenoe.

Genus *Perissoptera* Tate, 1865

Type species: *Rostellaria parkinsoni* Mantell, 1822, by subsequent designation, Cossmann, 1904. Albian, Europe.

Discussion: The genera *Perissoptera*, *Drepanocheilus* Meek, 1864, *Arrhoges* Gabb, 1868, *Latiala* Sohl, 1960, and *Graciliala* Sohl, 1960 (See Figure 8) have been considered to be closely related. Sohl (1960; 1967) placed *Perissoptera* and *Latiala* as subgenera of *Arrhoges*, and derived *Graciliala* from *Drepanocheilus*. Tate (1865), in proposing *Perissoptera* as a subgenus of *Aporrhais*, twice stated that the type species of a section of *Aporrhais* was *A. occidentalis* (Beck, 1836) (the species named by Gabb (1868) as type of *Arrhoges*) and wrote that this section corresponded with his new subgenus *Perissoptera*, which had characteristics intermediate between *Aporrhais* and *Alaria* Morris and Lycett, 1850. If Tate had actually designated *A. occidentalis* as type species of *Perissoptera*, his action would have preceeded Gabb's (1868) clear and unequivocal designation of *Chenopus occidentalis* (Beck, 1836) as type species of *Arrhoges*, and *Arrhoges* would be an objective junior synonym of *Perissoptera*.

Gabb (1868) commented upon Tate's paper in an addendum. He quoted Tate's "essential characters" of *Perissoptera* but considered it insufficiently distinct from *Anchura* Conrad, 1860, and did not mention that Tate had named *occidentalis* as type species of any group.

Gardner (1875, p. 51), who made no mention of Gabb's work, stated that Tate had designated *A. occidentalis* as type species of *Perissoptera*. Gardner argued, however, that there was no necessity for a supraspecific name for species better classed as *Aporrhais*, Group 1, and he did not use the binomen *Perissoptera occidentalis*. Gardner (1875) did not subsequently designate a type species for *Perissoptera* because he considered Tate to have named *A. occidentalis* as type species.

Cossmann (1904) recognized *Perissoptera* Tate as a useful taxon, in effect using it for Tate's Section I, *parkinsoni* group, and giving the type species as *Rostellaria parkinsoni* Mantell, 1822, Albian. Cossmann's footnote that refers to Tate's (1865) "fig. 18 (sub. nom. *Rost. Reussi*, non Geim.)" is part of the reference to Tate's proposal of the genus and apparently not part of Cossmann's designation of the type species. Cossmann (1904, p. 95) stated that his diagnosis of *Perissoptera* was based

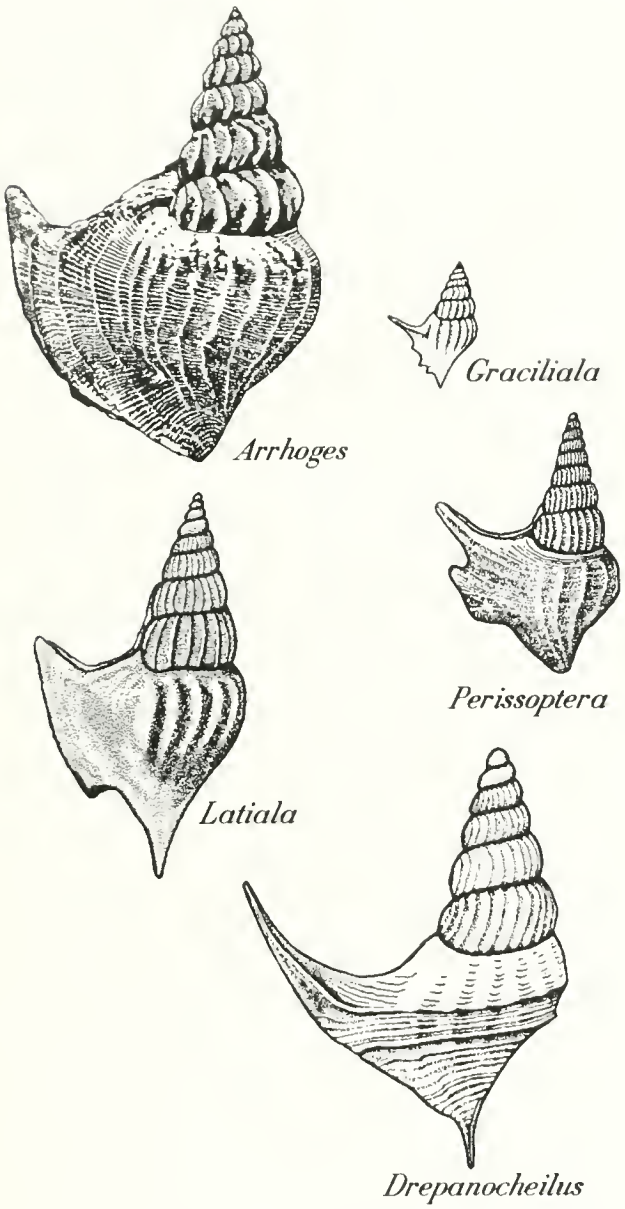


Figure 8. Line drawings of five aporrhaid genera, all ×1. Species serving as examples for the genera are: *Arrhoges occidentalis* (Beck, 1836), Recent, North Atlantic; *Graciliala calcaris* (Wade, 1926) Cretaceous, Gulf Coast; *Perissoptera parkinsoni* (Mantell, 1822), Cretaceous, England; *Drepanocheilus evansi* Cossmann, 1904, Cretaceous, Western Interior; *Latiala lobata* (Wade, 1926), Cretaceous, Gulf Coast.

on Gardner's (1875, pl. 66) figures of the type species and *Rostellaria marginata* Sowerby, 1836. *Rostellaria parkinsoni* Mantell, 1822, is the first species and *Rostellaria reussi* Geinitz, 1842, is the second species listed by Tate in his Section I, *Parkinsoni* group. Wenz (1940, p. 923) gave *Aporrhais (Perissoptera) reussii* Tate 1865 non Geinitz = *Rostellaria parkinsoni* Mantell as type of *Perissoptera*. Dockery (1993) gave the type species as *Rostellaria reussi* Tate original designation.

Tate (1865) did not directly designate any type species for *Perissoptera*. He wrote that *Aporrhais pespelecani* was the type species of the first section of *Aporrhais* and a second section of *Aporrhais* had for its type the living *A. occidentalis*., and later stated that *Perissoptera*, "intermediate between *Alaria* and *Aporrhais*, corresponds with that section of *Aporrhais* which has *A. occidentalis* as its type". In presenting his arrangement of the families Strombidae and Aporrhaiidae he included in Aporrhaiidae "the extinct genera *Alaria*, *Diarthema*, and *Perissoptera*." As Tate considered *Perissoptera* to be extinct, the Recent *A. occidentalis* could hardly "serve as" its type species.

Tate divided his new subgenus *Perissoptera* into three sections: Section I. *Parkinsoni* group; Section II. *Calcarata* group; and Section III. *Glabra* group. Tate's topic was the classification of Rostellariae of the Cretaceous rocks, and, as might be expected, *A. occidentalis*, a Recent species, is not included in any of Tate's three sections of *Perissoptera*. Thus, Tate not only did not directly designate *occidentalis* as type species of *Perissoptera*, but he actually excluded it as a possible type species by characterizing *Perissoptera* as extinct, and he did not list *A. occidentalis* among the species he included within *Perissoptera*.

Mantell (1822) provided the name *Rostellaria parkinsoni* for a specimen from the Albian of Blackdown figured by Parkinson (1811), but he also referred to a specimen of early Cenomanian age from the Grey Chalk. Tate (1865) mistakenly indicated that the Blackdown specimen was from the Grey Chalk and referred specimens from the Blackdown Greensand to *Aporrhais (Perissoptera) reussii* (Geinitz, 1842), but these are not *reussi* of Geinitz which is from the Baculitenschichten of Zatschke and is of Turonian age (Kollmann, 1978). Kollmann (1978) reviewed *Perissoptera parkinsoni*, discussed its occurrence, and considered the most repeated figure perporting to be *P. parkinsoni* (Mantell) (*i.e.*, Gardner, 1875, pl. 6, fig. 4; Wenz, 1940, p. 924, fig. 2705; etc.) to be an undescribed species, but both Kollmann (1978) and Tate (1865) quoted the same figures of Mantell (1822, pl. 18, fig. 1, 4, 5, 10) as being *Perissoptera parkinsoni* (Mantell, 1822).

Perissoptera has been widely used for moderately high spired aporrhaids having the axial sculpture much stronger than the spiral, and an expanded outer lip that is drawn out at its posterior extremity into a blade set off from the lobate medial distal margin by a sinus (Figure 8). The type species has a relatively short and wide rostrum and is moderately carinate on the last whorl. Included within *Perissoptera* are species with a longer rostrum and stronger spiral sculpture than are in *Arrhoges*, as well as a distinctive outer lip drawn out posteriorly and channeled interiorly. *Perissoptera* differs from *Latiala* in usually having the spiral sculpture stronger and in having the outer lip sinused on its distal margin, just anterior to the posterior extension, which is channeled interiorly.

Perissoptera occurs more commonly in Europe than

in America, although the genus is present in the Western Interior (*Perissopteria prolabiata* (White, 1876), Cenomanian) and the Gulf Coast (*Perissopteria prolabiata mississippiensis* Dockery, 1993, Campanian). The only species described from Pacific Slope deposits is *Perissoptera hannai* (Allison, 1955) from the Aptian-Albian Alisitos Formation of northern Baja California, Mexico.

Genus *Latiala* Sohl, 1960

Type species: *Anchura lobata* Wade, 1926, by original designation. Maastrichtian of the Gulf Coast of North America.

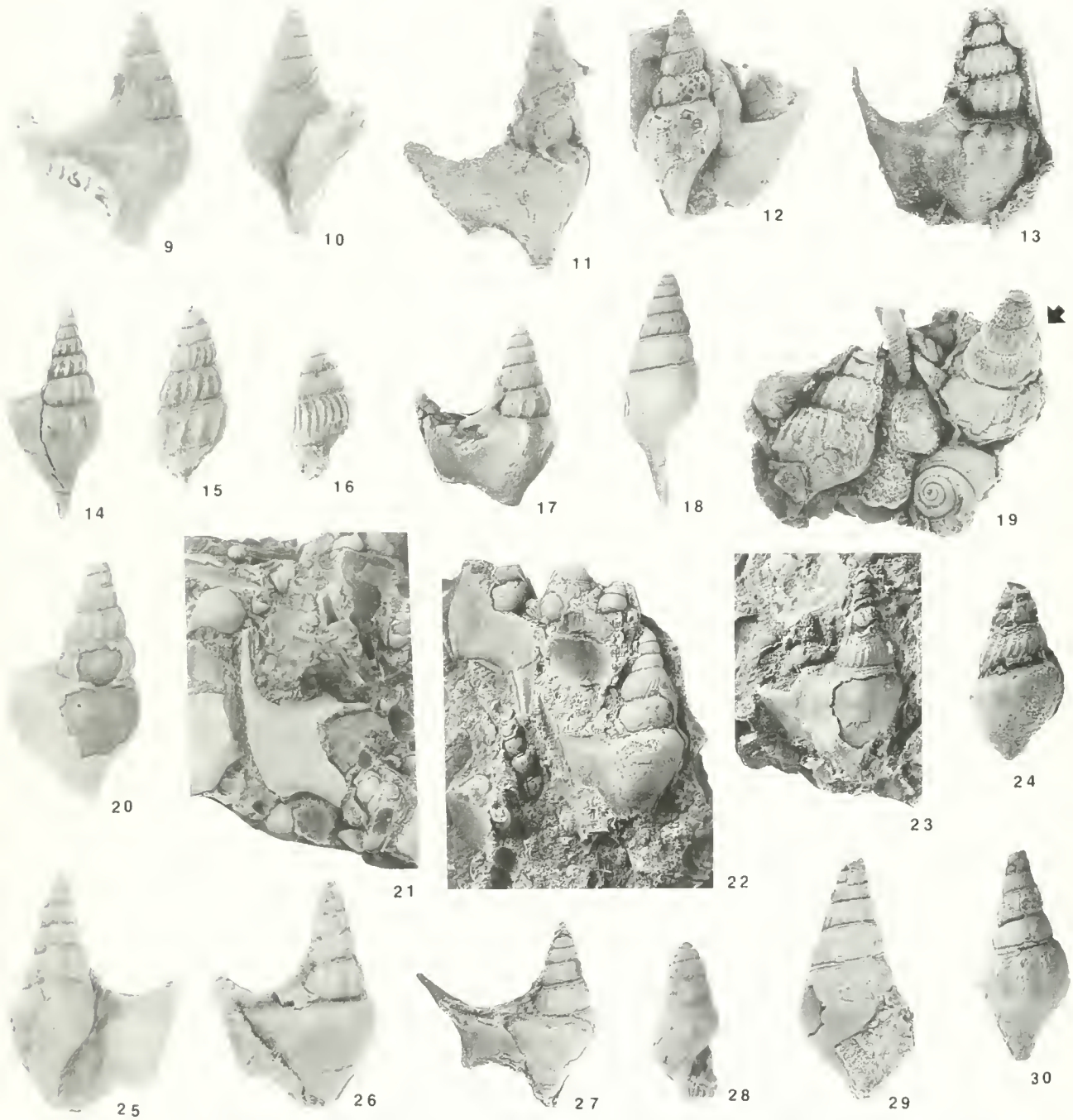
Discussion: Sohl (1960) differentiated *Latiala* from *Arrhoges* on the basis of *Latiala*'s broad, thick outer lip which is thickened and lobed at the anterior and posterior termini of its distal margin, the more pointed and longer lobe directed posteriorward and the blunter one directed anteriorward. He found *Latiala* to be widely distributed (*i.e.*, New Jersey, Tennessee, Mississippi, Texas, India, and South Africa) during the late Late Cretaceous. Abdel-Gawad (1986) has added *Latiala pelecyphora* (Kaunhowen, 1897) of late Maastrichtian age from the Middle Vistula Valley of Poland. Pacific Slope species resembling *Latiala* are, however, of Albian through Turonian age, and Kase (1984) reported Japanese *Latiala* of Aptian-Albian age. In Pacific Slope sediments, juvenile shells are more common and more abundant, especially in fine-grained, more off-shore deposits, than are the mature shells. Juvenile shells of *Latiala* appear to have been more readily transported into deeper water than shells of other gastropods with which the adult *Latiala* spp. are associated. Popenoe (1983), in assigning Pacific Slope specimens to *Latiala*, discussed only *A. (L.) californicus*, in which he included "*Alaria*" *nodosa* Packard and some specimens herein assigned to *L. heliaca* n. sp. and *L. sigma* n. sp.

Dockery (1993, p. 61) raised *Latiala* to a genus based on its having a thinner, more fragile shell than that of *Arrhoges*, a helicocone similar to that of *Graciliala*, and a body whorl without fine spiral lirae, but Roy (1994) did not separate *Latiala* from *Arrhoges*. Unlike *Graciliala*, but as in *Arrhoges*, the wing of *Latiala* is usually unchanneled. Specimens of *Latiala lobata* (Wade) from Coon Creek, Tennessee, show fine spiral striae under sufficient magnification even on the body whorl, but sculpture of Pacific Slope species does differ from that of the type species in having a few noticeably stronger lirae adjacent to the posterior suture. The Pacific Slope species herein assigned to *Latiala* vary in shell thickness; *L. californica* is thin shelled enough to meet Dockery's specifications, but *L. nodosa* has a thicker shell that is not more fragile than that of *Arrhoges*. All of these species have some development of spiral lirae on the body whorl, but in *L. californica* the lirae are so fine, and in *L. nodosa* the preservation of most specimens is sufficiently poor, that the lirae are commonly obliterated. *Latiala heliaca* has the strongest lirae, but they are not as strong as those of *Arrhoges occidentalis*. *Latiala heliaca* and *Latiala* sp. from Grave Creek are more slender and have a longer rostrum than *Arrhoges*. Of the five Pacific Slope *Latiala* species considered here, *L. nodosa* is most similar to *Arrhoges* in its stocky shape and thicker shell, but *L. nodosa* has the anterior and posterior wing extensions of *Latiala*, and its shape is similar to that of the thin shelled *L. sigma*, which has the longer rostrum and longer posterior wing extension of a *Latiala*. The most notable difference between these five species of *Latiala* lies in the sculpture of the spire and especially in the number and placement of axial ribs. A common feature of these species is the sculpture pattern on the spire of arched, somewhat opisthocline ribs crossed by fine spirals, a few of which are strongest adjacent to the posterior suture.

This sculpture pattern is one of the features that *Latiala* shares with, at least some species of *Perissoptera* Tate, 1865. In its early whorls, sculpture, and shape, exclusive of the wing, *Latiala* resembles *Perissoptera*. Wing development of more than one *Perissoptera* species passes through a stage in which the shape of the wing outline resembles that of *Latiala* or *Arrhoges*. A small specimen (Figures 9–10) in the LACM1P collections labeled *Perissoptera robinaldina* (d'Orbigny, 1843) from the Aptian of Atherfield, Isle of Wight, Great Britain (LACM1P loc. 11612), resembles Gardner's, 1875, pl. 7, fig. 11 of *P. robinaldina*. The distal margin of its wing is thickened anterior to a slight sinus at the base of the posterior wing digitation.

Although Sohl (1960) and Roy (1994) include *Latiala* as a subgenus of *Arrhoges*, and Sohl (1960) derives *Arrhoges* from *Drepanocheilus*, the species placed in *Latiala* by Kase (1984) and herein, suggest that *Latiala* appears in the geological record before *Arrhoges*, and *Arrhoges* might more reasonably be derived from *Latiala*. Dockery (1993) notes that the helicocones of *Graciliala* and *Latiala* are similar, but that *Graciliala* has a channeled outer lip and *Latiala* does not, a feature that lends support to Roy's (1994) placement of *Graciliala* nearer to *Drepanocheilus* than to *Arrhoges*. *Drepanocheilus* and *Perissoptera* have both been recorded from the Barremian by Roy (1994) and Kase (1980 in Kase and Maeda; but see remarks on *Perissoptera elegans* under *Aporrhais drachuki*) respectively; *Latiala* is first recognized in the Aptian (Kase, 1984); *Graciliala* apparently is known only from the Campanian and Maastrichtian; Sohl (1960) indicated that Cretaceous forms classed as *Arrhoges* belong either to *Latiala* or *Perissoptera*, and *Arrhoges* is present in the Paleocene (Kollmann and Peel, 1983).

Popenoe (1983) assigned *Latiala* from the Santa Ana Mountains to *Arrhoges (Latiala) californicus* which was described from the Siskiyou Mountains (Gabb, 1864). He also included in *A. (L.) californicus* specimens of Cenomanian to Turonian age which show considerable variation in number of axial ribs, height of spire, strength of spiral lirae, and length of rostrum. He evidently intended further study of this group as he had on hand



Figures 9–30. All whitened with ammonium chloride. **9–10.** *Perissoptera robinaldina* (d'Orbigny, 1842), hypotype LACMIP 11536, from Atherfield, Isle of Wight, Great Britain, ×2, **9,** back view, **10,** apertural view showing wing edge. **11–13, 19.** *Latiala* sp., all ×2, latex pulls from LACMIP loc. 24670, **11,** LACMIP 7969, back view, **12,** LACMIP 7968, apertural view, **13,** LACMIP 7966, back view, **19,** two specimens, arrow points to LACMIP 7967. **14–18, 20–21.** *Latiala heliaca* n. sp., **14,** holotype LACMIP 11378 from LACMIP loc. 28788, ×1, back view, **15,** paratype LACMIP 11379 from LACMIP loc. 28788, ×3, back view, **16,** paratype LACMIP 11380 from LACMIP loc. 28788, ×4, protoconch and first juvenile whorl, **17,** paratype LACMIP 11382 from LACMIP loc. 16838, ×2, back view, **18,** paratype LACMIP 11383 from LACMIP loc. 16838, ×2, left side, **20,** paratype 11381 from LACMIP loc. 16838, ×2, back view, **21,** paratype 11384 from LACMIP loc. 16838, ×2, wing in rock containing abundant *L. heliaca*. **22–30.** *Latiala californica* (Gabb), **22,** lectotype ANSP 4772 from the Siskiyou Mountains?, ×2, photo by T. Susuki, **23,** paralectotype ANSP 4772 from the Siskiyou Mountains?, ×2, photo by T. Susuki, **24,** hypotype LACMIP 11390 from LACMIP loc. 10901, ×2, back view, **25–26,** hypotype LACMIP 11388 from LACMIP loc. 10901, ×2, **25,** apertural view, **26,** back view, **27,** hypotype LACMIP 11385 from UCLA loc. 4365, ×2, back view, **28,** hypotype LACMIP 11387 from UCLA loc. 4365, ×3, apertural view, **29,** hypotype LACMIP 11386 from UCLA loc. 4365, ×2, apertural view, **30,** hypotype LACMIP 11389, from LACMIP loc. 10901, ×1.5, back view.

Table 4. Measurements in mm of specimens of *Latiala* sp.

	H	Hp	D	Dp	Dp/Hp	S	A	R	Rj	Rp	WB	WH	WD	Whorls
LACMIP 7966	18.2	3.3	—	—	—	9.1	—	—	18•?	15?	7.9	7.8	13.3	4
LACMIP 7628	19.0	3.0	—	—	—	10.0	30°	—	20•?	21?	6.5	—	—	5
LACMIP 7967	15.4	3.9	8.0	5.8	1.5	8.0	31°	8	21	24•	—	—	—	4
LACMIP 7969	20.5	3.8	—	6.8	1.8	11.0	28°	—	—	—	7.8	6.9	9•+	6

A = pleural angle; D = diameter last whorl; Dp = diameter of penultimate whorl; H = height; Hp = height penultimate whorl; R = axial ribs on body whorl; Rj = axial ribs on juvenile whorl; Rp = axial ribs on penultimate or other late teleoconch whorl; S = height of spire; WB = wing breadth measured from last rib to distal edge; WD = length distal margin of wing; WH = wing height except posterior and anterior spurs; † = broken, crushed; • = axial ribs counted on one side of whorl and doubled.

specimens of Cenomanian age from Clear Creek, Shasta County, and Sunflower Valley, Fresno County, that he had labeled *Arrhoges (Latiala)* new species. Specimens of *Latiala* of Turonian age from the Santa Ana Mountains reveal differences in the sculpture of the early whorls and in onset of sculpture changes on the spire, as compared to specimens of *L. californica* from the Siskiyou Mountains of the Oregon California border. On the basis of these differences, *L. californica* is discriminated from *L. nodosa* and considered not to be found in southern California.

Latiala sp.
Figures 11–13, 19; Table 4.

Diagnosis: A fusiform *Latiala* with about 18–24 axial ribs on spire whorls, reduced to about eight on body whorl; body whorl with ribs not confined to back of whorl.

Description: Shell of medium size, spindle shaped, except for expanded outer lip; whorls about twice as wide as high, numbering about seven or eight whorls, last whorl approximately half of shell height; pleural angle about 30°; whorl profile on spire roundly convex; profile of last whorl roundly convex except at axial nodes; outer lip expanded, broad, subquadrate, with short anterior and longer more pointed posterior projection. Protoconch unknown. Sculpture of 18–24 arched, round-topped, axial ribs, crossed by much weaker, fine spiral cordlets, strongest adjacent to posterior suture, two cordlets commonly strongest; sculpture on body whorl of eight to nine, short sharp, strong axial ribs crossed by fine spiral cordlets; ribs on back of body whorl shorter, stronger, more nodular. Aperture elongate; inner lip thickly callused with well defined edge; rostrum narrow, of moderate length.

Material examined: LACMIP 7628, 7966–7969 from LACMIP loc. 24670 on Grave Creek, Jackson County, Oregon.

Dimensions: See Table 4.

Age: Late early to middle Albian.

Geographic distribution: Studied specimens are all from the Hornbrook ? Formation on Grave Creek, Jackson County, Oregon

Remarks: This undescribed species is left unnamed because the specimens studied are all rock molds, and the figures are from latex pulls. The protoconch was present on some of these specimens, but the sandstone is too coarse-grained to yield a latex pull that replicates the original surface. Sculpture of the spire is similar to that of *Latiala hayamii* (Kase, 1984), but *Latiala* sp. has a broader pleural angle. *Latiala* sp. differs from *L. luciaca* in having more axial ribs on the body whorl, some of which are on the apertural side of the whorl. *Latiala* sp. has a proportionately higher wing than *Latiala heliaca, L. californica,* or *L. sigma.*

Table 5. Measurements in mm of specimens of *Latiala heliaca* n. sp.

	H	Hp	D	Dp	Dp/Hp	S	A	R	Rj	Rp	WB	WH	WD	Whorls
LACMIP 11378	34.1	4.6	—	8.9	1.9	16.0	35°	—	19	14	—	—	—	8
LACMIP 11379	9.7	1.9	5.0	4.2	2.2	—	34°	—	26•	—	—	—	—	7
LACMIP 11380	5.5	0.8	2.7	2.0	2.5	2.5	43°	—	38	—	—	—	—	5
UCLA 28625	20.5	3.3	9.6	7.0	2.1	11.6	32°	3	—	—	10.4	9	10	7
UCLA 28626	13.7	3.4	7.0	5.4	1.6	13.7	36°	—	30	17	—	—	—	9
LACMIP 11381	19.2	3.3	8.4	6.0	1.8	9.8	35°	3	—	—	—	—	—	5
LACMIP 11382	14.5	2.4	6.8	4.9	2.0	6.0	35°	2	—	14	6.6	5.5	7.0	6
LACMIP 11383	17.0	2.7	6.8	5.2	1.9	8.6	34°	—	28•	—	—	—	—	8
LACMIP 11384	—	—	—	—	—	—	—	—	—	—	7.8	7.3	14.8	—

A = pleural angle; D = diameter last whorl; Dp = diameter of penultimate whorl; H = height; Hp = height penultimate whorl; R = axial ribs on body whorl; Rj = axial ribs on juvenile whorl; Rp = axial ribs on penultimate or other late teleoconch whorl; S = height of spire; WB = wing breadth measured from last rib to distal edge; WD = length distal margin of wing; WH = wing height except posterior and anterior spurs; • = axial ribs counted on one side of whorl and doubled.

Latiala heliaca n. sp.
Figures 14–18, 20–21; Table 5.

Arrhoges californicus (Gabb)—Murphy and Rodda, 1960, p. 841, pl. 102, fig. 6–7.

Diagnosis: A slender fusiform *Latiala* with about 16 axial ribs on spire whorls, greatly reduced on final whorl to two or three on dorsal side of body whorl.

Description: Shell of medium size, spindle shaped, except for expanded outer lip, of about nine whorls; whorls about twice as wide as high; last whorl approximately half of shell height; pleural angle about 36°; whorl profile on spire roundly convex; profile of last whorl roundly convex except at axial nodes and with broad axial bulge on apertural face; outer lip expanded, broad, subquadrate, slightly thickened at distal edge, with short anterior and longer posterior projections. Protoconch of four or five rapidly enlarging, rounded, glossy whorls; transition to juvenile sculpture gradual, marked by spaced faint, arched, axial ribs and spiral striae; ribs rapidly strengthened, becoming crowded. Sculpture on first juvenile whorl of 26–36 arched axial ribs crossed by much weaker fine spiral cordlets; sculpture of next through penultimate whorls of about 16 arcuate axial ribs crossed by fine spiral cordlets, strongest adjacent to posterior suture, three cordlets commonly strongest; sculpture on body whorl of three to four short, sharp, strong axial ribs crossed by fine spiral cordlets. Aperture elongate; inner lip broadly callused, callus angling from posterior of aperture across mid-whorl on apertural face and wrapping halfway around anterior rostrum; rostrum narrow, straight, relatively short.

Type specimens: Holotype, LACMIP 11378. Paratypes LACMIP 11379–11380 from LACMIP loc. 28788; UCLA 28625 = LACMIP 9825 , UCLA 28626 = LACMIP 9824 from UCLA loc. 3465, and LACMIP 11381–11384 from LACMIP loc. 16838, Ono area, Shasta County, California.

Type locality: LACMIP 28788, north end of Sunflower Valley (=McLure Valley), Fresno County, California. Panoche Formation.

Dimensions: See Table 5.

Age: ?Late Albian-Cenomanian.

Geographic distribution: Budden Canyon Formation, Bald Hills Member, Ono area, Shasta County (UCLA loc. 3465; Great Valley Series, Elder Creek, Tehama County (LACMIP loc. 24370); Panoche Formation, Sunflower Valley, Fresno County (LACMIP loc. 28788), California.

Remarks: No varices were recognized on the early whorls of *L. heliaca*. LACMIP 11380 consists of a protoconch of 4 polished, rounded whorls and the first teleoconch whorl. The earliest axial ribs are irregular, low, and difficult to count, but on the second quarter of the first teleoconch whorl the ribs become stronger, more distant and more regular. Rib strength varies between

Table 6. Measurements in mm of specimens of *Latiala californica* (Gabb).

	H	Hp	D	Dp	Dp/Hp	S	A	R	Rj	Rp	WB	WH	WD	Whorls
ANSP 4272	15.0	2.0	5.0	3.9	1.95	7.0	?	—	40	—	4.7	3.8	7.0	7
CASG 61950.01	10.65		6.15											
CASG 61950.02	22.26													
LACMIP 11385	14.8	2.0	6.0	4.7	2.35	7.0	42°	3	30+	—	7.0	5.0	6.5	7
LACMIP 11386	19.7	3.8	8.5	6.5	1.76	11.0	30°	4	—	20	—	—	—	6
LACMIP 11387	8.9	1.8	4.3	3.3	1.83	—	33°	—	§	—	—	—	—	6
LACMIP 11388	18.3	3.4	7.9	6.0	1.76	10.0	35°	3	—	14?	8.8	6.9	9.0	8
LACMIP 11389	22.3	3.4	9.6	6.9	2.03	10.5	34°	4	60?	—	—	—	—	5
LACMIP 11390	14.0	3.4	7.0	5.7	1.7	8.0	34°	3	—	22	—	—	—	4

A = pleural angle; D = diameter last whorl; Dp = diameter of penultimate whorl; H = height; Hp = height penultimate whorl; R = axial ribs on body whorl; Rj = axial ribs on juvenile whorl; Rp = axial ribs on penultimate or other late teleoconch whorl; S = height of spire; WB = wing breadth measured from last rib to distal edge; WD = length distal margin of wing; WH = wing height except posterior and anterior spurs; § = ribs too fine to count.

individuals, and on some whorls the axial ribs may be indiscernible.

Specimens from Elder Creek (LACMIP loc. 24370) are from a boulder containing species suggestive of late Albian age in a conglomerate that is of Turonian age (Jones and Bailey, 1973).

Latiala heliaca is larger and more slender than *L. californica* and has fewer axial ribs. Whereas *L. californica* retains the fine axial ribbing of the juvenile whorl throughout most of the spire whorls, in *L. heliaca* the intermediate whorls have fewer, coarser ribs, and the body whorl is not angulate at the shoulder, although the nodose axial ribs can create the impression of a shoulder angulation. *Latiala helica* has more axial ribs on the spire and fewer on the body whorl, is more slender with a more fusiform shape, and has a slightly broader shorter wing than *L. nodosa*. *Latiala helica* is more slender, has less of a shoulder, fewer axial ribs, and a shorter wing than *L. sigma*.

Latiala heliaca is most similar in shape to *Latiala hayamii* (Kase, 1984) from the Aptian-Albian of northeast Japan, but differs in having fewer axial ribs on the body whorl.

Etymology: The species name, derived from Greek, *helios*, sun, refers to the type locality at the northwest end of Sunflower Valley.

Latiala californica (Gabb, 1864)
Figures 22–30; Table 6.

Aporrhais californica Gabb, 1864, p. 128, pl. 29, figs. 230a, b.
Arrhoges californicus (Gabb)—Stewart, 1927, p. 363, pl. 21, fig. 15.
Arrhoges (Latiala) californicus (Gabb). Popenoe, 1983, p. 761 (in part; not fig. 6F, 1 See *L. nodosa* Packard).
Not *Arrhoges californicus* (Gabb)—Murphy and Rodda, 1960, p. 841, pl. 102, fig. 6–7. See *L. heliaca* n. sp.
Not *Arrhoges californicus* (Gabb)—Jones, Sliter and Popenoe, 1978, p. xxii.9, pl. 1, fig. 10. See *L. nodosa* Packard).

Diagnosis: A small *Latiala* in which axial sculpture of spire consists of fine, closely spaced, almost sigmoid ribs. Sculpture of body whorl of three to four strong, short ribs, present only on dorsal side, nodular at the shoulder.

Description: Shell, thin, of small to medium size, spindle shaped except for expanded outer lip; whorls nearly twice as wide as high, numbering about seven; last whorl approximately two-thirds to three-quarters of shell height; pleural angle about 35°; whorl profile on spire rounded; profile of last whorl angulate at shoulder and with broad axial bulge on apertural face; varices rare (?one juvenile varix per specimen), forming broad axial swellings; outer lip expanded, broad and moderately tall, with very short anterior and much longer posterior projections. Protoconch multispiral of five or six smooth, rounded whorls. Sculpture on body whorl of about four short, nodular axial ribs on dorsal side, a broad axial bulge on the apertural side and fine spiral striae, stronger spiral cordlets on shoulder and on collar; sculpture

on penultimate whorl of about 20 fine nearly sigmoid axial ribs and fine (about four per mm), regularly spaced spiral cordlets, strongest near posterior suture; sculpture on earlier whorls finer than on penultimate whorl. Aperture elongate, outer lip thickened internaly; distal edge of outer lip relatively long; rostrum short.

Type specimens: Lectotype ANSP 4272 (designated by Murphy and Rodda, 1960). Paralectotypes (2) ANSP 79470; CASG 61950.01 (one loose specimen + a rock fragment containing several, two largely exposed).

Hypotypes: LACMIP 11385–11388 from UCLA loc. 4365, Redding area, Shasta County; and LACMIP 11388–11390 from LACMIP loc. 10901, Rancheria Gulch, Siskiyou County, California.

Type locality: Siskiyou Mountains?, Jackson County, Oregon or Siskiyou County, California. Gabb (1864, p. 129) listed this species from "Orestimba Cañon; Martiñez; Puerto Cañon, Stanislaus County; Siskiyou Mountains." None of these was precise as to geographic or stratigraphic position. Stewart (1927) said that the label with Gabb's ANSP specimens read Siskiyou Mts. and Martinez, but that all of the specimens were in a similar black limestone matrix with small pebbles which he considered more likely to have come from the Siskiyou Mountains than from Martinez. Natural History Museum of Los Angeles County specimens resembling Gabb's material are from the Osburger Gulch Sandstone Member of the Hornbrook Formation in the Siskiyou Mountains, but are not identical in preservation to Gabb's Siskiyou Mountains specimens.

Dimensions: See Table 6.

Age: Turonian.

Geographic distribution: Hornbrook Formation, Osburger Gulch Sandstone Member (LACMIP loc. 10901, LACMIP loc. 10876, LACMIP loc. 25422), Jackson County, Oregon and Siskiyou County, California; Redding Formation, ?Frazier Siltsone Member (UCLA 4365) near Redding, Shasta County, California.

Remarks: The CASG "syntypes" have a label that lists SUT 266, Calif. Geol. Surv. 2144, and UCB 14907, indicating that the specimens were originally at University of California, Berkeley, Museum of Paleontology before they were moved to Stanford and from there to the California Academy of Sciences.

The lectotype is 15 mm high, nearly complete, and has an adult aperture, but is missing shell on the last two whorls. The absence of parts of the shell interfers with describing the sculpture. The ANSP and CASG type specimens are small, but some collections (*e.g.*, LACMIP loc. 10901) contain a few larger individuals (Figure 30). The above description depends in part on additional specimens from the rather generalized type locality of Siskiyou Mountains. Specimens are commonly found locally in abundance as in the blocks of paratype material, but the very thin shell of this species has made difficult the recovery of specimens with shell adhering. This species exhibits juvenile sculpture onto the penultimate whorl on small adults and up to the penultimate whorl on large adults.

Gabb's illustration (fig. 230a) has an outline more like that of *Latiala heliaca* than of *L. californica* and may have been based on a specimen of that species. If so, the specimen appears to have been lost.

Latiala californica differs from *L. heliaca* in having an angulate shoulder and more axial ribs on most whorls. It differs from *L. nodosa* in having a very thin shell, retaining the fine axial ribbing onto or up to the penultimate whorl. *Latiala californica* is smaller, has weaker spiral sculpture, and fewer axial ribs on the body whorl than *L. sigma*. Of the five species discribed in this paper, *L. californica* has the relatively shortest wing.

Latiala sigma n. sp.
Figures 31–43; Table 7.

Diagnosis: A relatively large *Latiala* with relatively strong spiral sculpture, numerous fine axial ribs on early whorls, and about seven ribs on body whorl.

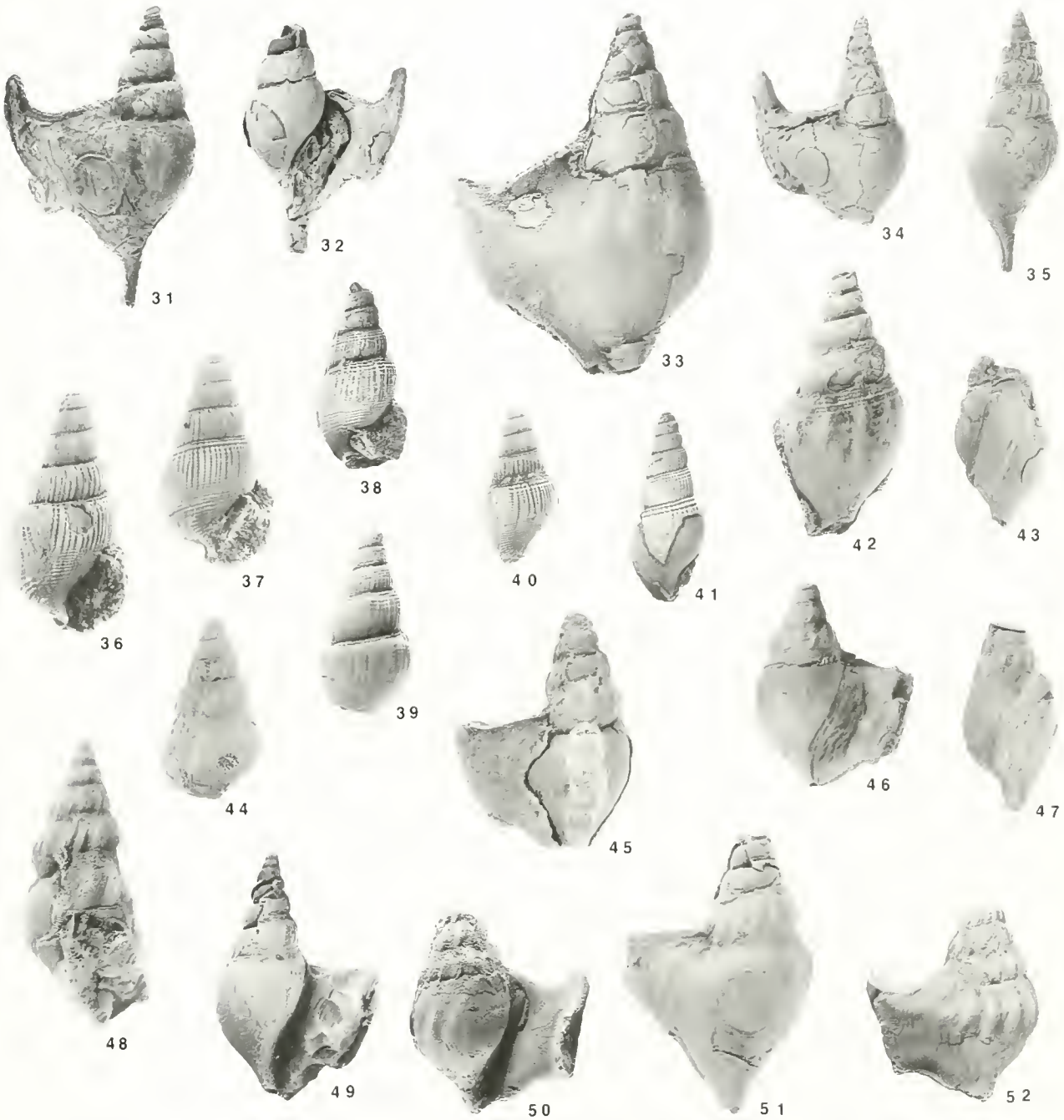
Description: Shell of medium size, stoutly spindle shaped, except for expanded outer lip; whorls about twice as wide as high, nine in large mature individuals, seven in small mature individuals; last whorl approximately two-thirds of shell height; pleural angle about 36°; whorl profile on spire nearly flat sided with narrow rounded shoulder; whorl profile of last two whorls rather evenly rounded; varices poorly developed on early whorls; outer lip expanded, tall and broad, subquadrate with very short, blunt anterior and narrow posterior projections; angle of distal edge of outer lip to that of shell axis about 33°. Protoconch of four rounded, glossy whorls. Sculpture on winged body whorl of five to seven short axial ribs on dorsal side, on penultimate whorl of about 20 to 30 curved axial ribs and three narrow spiral cordlets at the suture; sculpture on first quarter of first teloconch whorl of fine axial lines, at least eight per 1 mm, axial lines double in size and by third teleoconch whorl are four to 1 mm; second teleoconch whorl with about 40–50 fine axial ribs crossing about 20 spiral cordlets; cordlets weakest mid whorl and strongest posteriorly. Aperture elongate, outer lip not much thickened; inner lip somewhat thickened; rostrum relatively long.

Type specimens: Holotype LACMIP 11391. Paratypes LACMIP 11392–11398 from UCLA loc. 5421, LACMIP 11399–11401 from CIT 1346, and LACMIP 11402 from CIT 1266, all on Little Cow Creek, Redding area, Shasta County, California.

Type locality: UCLA loc. 5421, Little Cow Creek, south line sec. 9, T32N, R3W, Millville quad., Shasta County, California. Redding Formation, Melton Sandstone.

Dimensions: See Table 7.

Age: Turonian.



Figures 31–52. All whitened with ammonium chloride. **31–43.** *Latiala sigma* n. sp., **31,** holotype LACMIP 11391 from UCLA loc. 5421, ×1.5, back view, **32,** paratype LACMIP 11392 from UCLA loc. 5421, ×1, apertural view, **33,** paratype LACMIP 11400 from CIT loc. 1346, ×1.5, back view, **34,** paratype LACMIP 11393 from UCLA loc. 5421, ×1, back view, **35,** paratype LACMIP 11402 from CIT loc. 1266, ×1.5, showing juvenile to mature sculpture, **36,** paratype LACMIP 11396 from UCLA loc. 5421, ×4, protoconch and two juvenile whorls, **37,** paratype LACMIP 11398 from UCLA loc. 5421, ×4, protoconch and two juvenile whorls, **38–39,** paratype LACMIP 11394 from UCLA loc. 5421, ×2, juvenile whorls, **40,** paratype LACMIP 11397 from UCLA loc. 5421, ×3, protoconch, two juvenile whorls, and a varix, **41,** paratype LACMIP 11395 from UCLA loc. 5421, ×2, protoconch and three juvenile whorls, **42,** paratype LACMIP 11401 from CIT loc. 1346, ×1.5, showing mature sculpture on last whorl, **43,** paratype LACMIP 11417 from UCLA loc. 5421, ×1, angle of outer lip. **44–52.** *Latiala nodosa* (Packard), hypotypes, **44,** LACMIP 11406 from CIT loc. 1065, ×3, protoconch and three juvenile whorls, **45,** LACMIP 11403 from CIT loc. 1164, ×1.5, back view, **46,** LACMIP 11408 from CIT loc. 1532, ×1, apertural view, **47, 50, 52,** LACMIP 10808 (=UCLA 58438) from CIT loc. 1212, ×1, **47,** wing angle, **50,** apertural view, photo by T. Susuki, **52,** back view, photo by T. Susuki, **48,** LACMIP 11407 from CIT loc. 1212, ×2, juvenile to mature sculpture, **49,** LACMIP 11405 from CIT loc. 1164, ×1.5, apertural view, **51,** LACMIP 11404 from CIT loc. 1164, ×1.5, back view.

Table 7. Measurements in mm of specimens of *Latiala sigma* n. sp.

	H	Hp	D	Dp	Dp/Hp	S	A	R	Rj	Rp	WB	WH	WD	Whorls
LACMIP 11392	35.2†	6.5	13.0	10.9	1.7	13.4	40°	—	—	—	16.8	13.5	18.7	3
LACMIP 11393	34.4	6.0	14.0	?	—	19.4	?	?	—	—	17.4	14.0	16.0	5
LACMIP 11391	32.4	5.0	12.0	8.8	1.8	13.5	42°	7	—	—	12.0	10.8	15.5	5
LACMIP 11394	14.6	3.8	—	5.6	1.5	—	31°	—	38•	—	—	—	—	4
LACMIP 11395	14.8	3.2	—	5.4	1.7	—	35°	—	60•	—	—	—	—	4
LACMIP 11396	9.5	2.0	—	3.7	1.8	—	34°	—	60•	—	—	—	—	6
LACMIP 11397	8.5	1.7	—	3.0	1.8	—	35°	—	58	—	—	—	—	6
LACMIP 11398	8.7	1.8	—	3.6	2.0	—	34°	—	58	—	—	—	—	5
LACMIP 11399	18.4	3.9	9.3	6.6	1.7	9.6	35°	4?	—	—	—	—	—	4
LACMIP 11400	38.0	7.0	16.9	12.2	1.7	19.0	35°	6+	—	—	13.9	13.9	—	6
LACMIP 11401	29.8	5.0	13.8	10.7	2.1	14.6	37°	6	—	—	—	—	—	5
LACMIP 11402	29.0	4.5	10.7	7.9	1.8	13.8	32°	—	38•	—	—	—	—	6

A = pleural angle; D = diameter last whorl; Dp = diameter of penultimate whorl; H = height; Hp = height penultimate whorl; R = axial ribs on body whorl; Rj = axial ribs on juvenile whorl; Rp = axial ribs on penultimate or other late teleoconch whorl; S = height of spire; WB = wing breadth measured from last rib to distal edge; WD = length distal margin of wing; WH = wing height except posterior and anterior spurs; • = axial ribs counted on one side of whorl and doubled.

Geographic distribution: Redding Formation, Melton Sandstone, Redding area, Shasta County, California. [CIT loc. 1264; CIT loc. 1265; CIT loc. 1266; CIT loc. 1346 = UCLA loc. 5421]

Remarks: *Latiala sigma* has the strongest spiral sculpture and longest rostrum of the *Latiala* discussed herein. All of the available mature specimens have the shell badly leached and the adult whorl surface is not preserved on any of them. Winged adults range in size from about 22 mm high to 46 mm high. None of the available specimens shows evidence of thickening along the distal margin of the wing. Obscure swellings that may be indistinct varices are present on some early whorls. *Latiala sigma* has a more gradate spire, more axial ribs on the immature whorls, and the distal edge of the wing is at a greater angle to the shell axis than in *L. nodosa*. It is larger, has a broader wing, and has more axial ribs on its body whorl than *L. californica* and *L. heliaca*.

Etymology: *Sigma*, the eighteenth letter of the Greek alphabet, was W. P. Popenoe's manuscript name for this species.

Latiala nodosa (Packard, 1922)
Figures 44–52; Table 8.

Alaria nodosa Packard, 1922, p. 430, pl. 36, figs. 5a-5b.
Arrhoges californicus (Gabb)—Jones, Sliter and Popenoe, 1978, p. xxii.9, pl. 1, fig. 10.
Arrhoges (Latiala) californicus (Gabb)—Popenoe, 1983, p. 76 (in part), fig. 6 F, I.

Diagnosis: A thick-shelled *Latiala* with about four teleoconch whorls having 14 oblique axial ribs per whorl, seven to eight axial ribs on body whorl not restricted to back of whorl, and a broad wing.

Description: Shell thick for a *Latiala*, of medium size, spindle-shaped, except for expanded mature labrum; whorls twice as wide as high, numbering about nine; last whorl a little over half of shell height; pleural angle about 37°; whorl profile on spire rounded but ribs create incipient shoulder; profile of last whorl rounded but with apparent angulation caused by nodes; commonly one varix per submature whorl; outer lip expanded, moderately broad, subquadrate with short anterior and posterior projections; angle of distal edge of outer lip to that of shell axis about 22°. Protoconch of four smooth rounded whorls. Sculpture on fifth and sixth whorl of about 20 low, oblique, gently concave to aperture, crested axial ribs, on penultimate whorl of 14 axial ribs; body whorl sculptured by seven to eight axial ribs forming nodose shoulder; all postprotoconch whorls with fine spiral striae, strongest near the posterior suture. Aperture elongate, outer lip thickened and not channeled; callus deposit over apertural face of body whorl extending as broad tongue over penultimate whorl to posterior suture; inner lip thin edged, medially thickened; rostrum short.

Type specimens: Holotype UCBMP 12297. Paratype

Table 8. Measurements in mm of specimens of *Latiala nodosa* (Packard).

	H	Hp	D	Dp	Dp/Hp	S	A	R	Rj	Rp	WB	WH	WD	Whorls
UCLA 58438	31.5	5.5	16.9	12.0	2.2	12.0	32°	9	—	15	15.6	14.8	17.0	3
LACMIP 11403	24.7†	5.5	11.5†	9.0	1.6	14.0†	30°	—	?.	14	11.8	11.2	12.0†	5
LACMIP 11404	29.8†	5.8	13.0	9.8	1.7	12.6†	38°	4	—	17	11.4†	—	—	4
LACMIP 11405	26.4†	4.4	11.0	8.2	1.9	13.8	36°	7	?.	14•	9.8	10.0	11.3†	7
LACMIP 11406	9.9	1.9	5.5	4.0	2.1	—	34°	—	20•	—	—	—	—	6
LACMIP 11407	23.0	3.8	—	9.0	2.4	—	42°	—	20	14	—	—	—	7
LACMIP 11408	31.8	4.9	14.3	11.4	2.32	13.5	40°	6	—	16•	13	16	17.7	4
LACMIP 11409	35.5	5.8	16.0	12.0	2.06	16.4	40°	11	—	16•	—	—	—	5

A = pleural angle; D = diameter last whorl; Dp = diameter of penultimate whorl; H = height; Hp = height penultimate whorl; R = axial ribs on body whorl; Rj = axial ribs on juvenile whorl; Rp = axial ribs on penultimate or other late teleoconch whorl; S = height of spire; WB = wing breadth measured from last rib to distal edge; WD = length distal margin of wing; WH = wing height except posterior and anterior spurs; † = broken, crushed; • = axial ribs counted on one side of whorl and doubled.

UCBMP 12296 from UCBMP loc. 2142, Santa Ana Mts., Orange County, California.

Hypotypes: UCLA 58438 (=LACMIP 10808) (*A. (L.) californicus* of Popenoe) from CIT loc.1212 (=LACMIP loc.10735), LACMIP 11407 from CIT loc. 1221, and LACMIP 11408–11409 from CIT loc. 1532, Redding area, Shasta County; LACMIP 11403–11405 from CIT loc. 1164, Santa Ana Mountains, Orange County, California.

Type locality: UCBMP loc. 2155, 5.43 km S 65°E of B.M. 610, Corona sheet. 0.8 km from mouth of Black Star Cañon. Chico float.

Dimensions: See Table 8.

Age: Turonian.

Geographic distribution: Ladd Formation, Baker Canyon Sandstone and lower Holz Shale Members, Santa Ana Mountains, Orange County, California, (CIT loc. 80, 1 spec.; CIT loc. 82, 12 spec.; CIT loc. 99, 2 spec.; CIT loc. 454, 1 spec.; CIT loc. 1065, 4 immature spec.; CIT loc. 1164, 59 spec.; CIT loc. 1290, 1 spec.; CIT loc. 1307, 8 spec.; UCLA loc. 2325, 2 spec.; LACMIP loc. 10953, 1 spec.; LACMIP loc. 29181, 1 spec.); Redding Formation, Frazier Silt, Redding area, Shasta County, California, (CIT loc. 1212, 16 spec.); CIT loc. 1221, 3 spec.; CIT loc. 1532, 14 spec.; UCLA loc. 4658, 15 spec.).

Remarks: Precise stratigraphic position of the holotype was unknown to Packard (1922), but the paratypes are from UCBMP loc. 2142, which is in the lower Holz Shale. The species has been collected from numerous localities in the Baker Canyon Sandstone and lower Holz Shale Members of the Ladd Formation.

Popenoe (1983) included *L. nodosa* in *A. (L.) californicus*, but the early whorls of *L. nodosa* have fewer axial ribs per whorl, the earliest of which are so low that the spiral riblets adjacent to the posterior sculpture is the more noticeable sculptural element. The early axial ribs of *L. nodosa*, are characteristically distant and crested with the sharp slope toward the aperture. *Latiala nodosa* has axial ribs on the apertural face of the body whorl but *L. californica* does not, and *L. californica* has a better-defined shoulder and fewer varices on the early whorls. Although *L. nodosa* is common to abundant at more than four localities, few specimens have the earliest whorls well-preserved. LACMIP 11406 and other specimens from CIT loc. 1065 have well-preserved early sculpture; LACMIP 11407 appears to have nearly all of the early whorls, but the shell surface of the first four whorls is not preserved. Remnants of fine axial ribs are present on the fifth whorl and 14 ribs are on the sixth whorl. The fifth whorl has two ribs for each rib on the sixth whorl. Callus on the apertural face of the body whorl is thick enough to obscure some of the axial ribs and forms a broad lump at the base of the body whorl adjacent to the aperture. It extends apically from the posterior end of the aperture forming a callus tongue

across the penultimate whorl. A thin and fairly narrow inner lip is developed over the callus.

Redding area specimens of *L. nodosa* are larger, more robust, and have a wider pleural angle than those from the Santa Ana Mountains. In the Redding area, *L. nodosa* and *L. sigma* are of similar size, but *L. nodosa* has a thicker shell, a more quadrate wing, the distal edge of which is at a lower angle to the shell axis, and early whorls with fewer axial ribs and weaker spiral striae. *Latiala nodosa* is from the Frazier Silt but *L. sigma* is from the Melton Sandstone. Of the five species of *Latiala* described in this paper, *L. nodosa* has the tallest wing relative to breadth and to shell height.

Genus *Alarimella* new genus

Type species: *Aporrhais vetus* Packard, 1922 from the Turonian of southern California.

Diagnosis: A *Rimella*-like aporrhaid with sculpture of nearly aligned axial ribs and finer spiral cords but with an expanded outer lip. Whorls becoming carinate on body whorl; carina extending along trigonally expanded outer lip; outer lip with a posterior digitation proximal or adnate to the spire; interior of outer lip channeled opposite the carina.

Discussion: *Alarimella* is very similar in shape and sculpture to some strombids such as the *Rimella*-like gastropods (Clark and Palmer, 1923) of the Rostellariinae (Delpey, 1941). Certain species of *Calyptraphorus* Conrad, 1857, e. g., *Calyptraphorus binodiferus* Perrilliat and Vega, 1997, Maastrichtian, southern Mexico, also have similar shape and sculpture beneath their mature callus covering. The shape of the aperture and extension of the posterior canal up the spire of *Alarimella* also are similar in these strombids. The most obvious difference is in the outer lip of *Alarimella* which is alately expanded and interiorly channeled but in the *Rimella*-like strombids is not. Additionally the aperture of aporrhaids has sinus areas on either side of the rostrum and a concave columella which accomodate the anterior end of the foot and the snout, but the strombid shell is less excavated across the anterior end of the columella. Strombs characteristically have a strombid notch near the anterior end of the outer lip which is used by the stalked eye of strombs (Abbott, 1960). The eyes of aporrhaids are on bulbs at the tentacle bases (Yonge, 1937) rather than on long, mobile pedicle tips and are not extendible as in the strombs. Possibly stalked eyes evolved in advance of the notch through which they extend, and absence of the strombid notch does not assure aporrhaid eyes. The strombid notch is not always well defined in strombs (Savazzi, 1991), and some of the *Rimella*-like gastropods are said not to have a strombid notch, e. g. *Rimella* Agassiz, 1840, *Macilentos* Clark and Palmer, 1923 (subobsolete fide Clark and Palmer, 1923, lacking fide Vokes, 1939), *Couclitzia* Clark and Palmer, 1923. Nonetheless, the absence of a strombid notch in *Alarimella* in conjunction with the similarity of the sculpture of *Alarimella* on the whorls of the spire to that of *Latiala*, *Perissoptera*, and *Graciliala*, the development on the body whorl of *Alarimella* of a modest carina, and the possession by *Alarimella* of an expanded outer lip that is internally channeled opposite the carina suggest that it be included in Aporrhaiidae.

Varices on spires of *Alarimella veta* and A. *anae* are similar to those on species of *Rimella*. Varices are said to be of little or no systematic importance in Strombaceans (e. g. Davies, 1971, p. 328), and their presence does not aid in differentiating between Aporrhaidae and Strombidae, but Clark and Palmer (1923) thought their absence on *Macilentos* characteristic.

As in several aporrhaids (e. g., *Latiala*) the sculpture on the body whorl of *Alarimella* not only differs from that on the spire, but the back of the body whorl has fewer and stronger ribs than the previous whorl, and on the apertural face, ribs may be virtually absent. A similar pattern of enlarged nodes on the back of the body whorl appears to be present in *Calyptraphorus binodiferus* and in some of the *Rimella*-form gastropods (*e.g., Rimella*). Savazzi (1991) suggests that such enlarged nodes assist an animal that has landed aperture up to right itself.

Length and deployment of the posterior canal is considered a supraspecific characteristic among the *Rimella*-like gastropods (Clark and Palmer, 1923). None of the specimens of A. *veta* has a complete spire, but the posterior canal appears to end on the juvenile whorls, and the canal of a specimen of A. *anae*, which has probably not reached its full length, does not extend to the tip of the spire nor does it change direction and extend across the back of the spire as in *Calyptraphorus binodiferus*. *Alarimella* is sufficiently similar to *Rimella*-like gastropods, except for the expanded outer lip, to suggest that *Rimella*, may be derived from *Alarimella* by the reduction of the outer lip and lengthening of the posterior canal. Similarity of sculpture of *Calyptraphorus binodiferus* to that of A. *veta* suggests that *Calyptraphorus* Conrad, 1857, might also derive from an *Alarimella*-like form by reduction of the outer lip, lengthening of the posterior canal, and increase of callus deposition over the shell. Roy (1996) indicated that strombids originated within the aporrhaids during Cenomanian-Turonian times, which places *Alarimella* near the time of divergence.

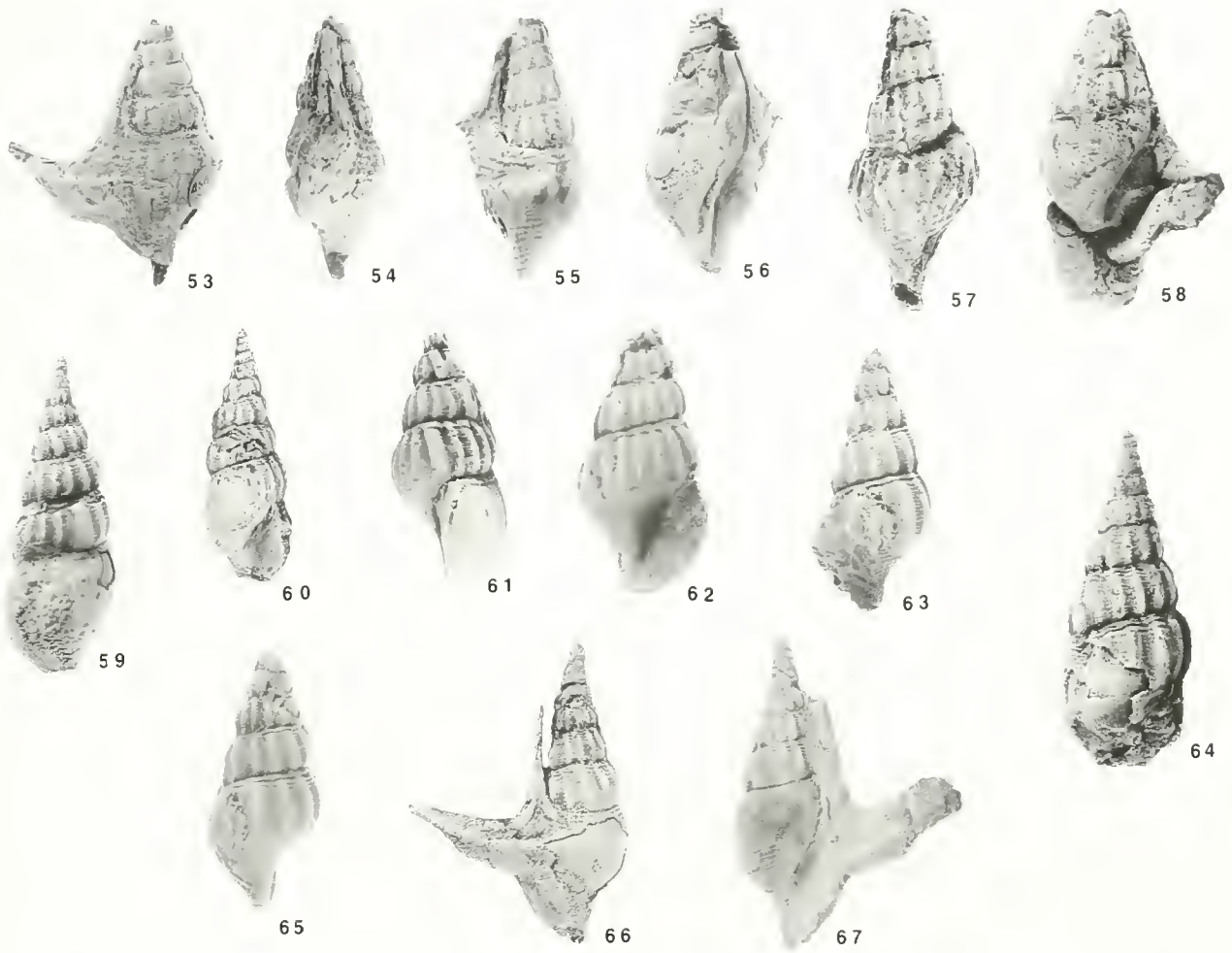
Figures in Korobkov et al. (1960, p. 188) of *Pugioptera subrequieni* Pchelintsev, 1953 from the Turonian of Transcaucasia are suggestive of *Alarimella*, but *Rostellaria requieniana* d'Orbigny, 1842, the type species of *Pugioptera* Pchelintsev, 1953, is an *Anchura* Conrad, 1860 (Korobkov et al., 1960, p. 183 have *Rostellaria requemana* as type species, a misspelling of *R. requieniana* spelled correctly on page 187 in the explanation for Figure 453).

Etymology: *Ala* wing, Latin and *Rimella* a gastropod.

Alarimella veta (Packard, 1922)
Figures 53–58; Table 9.

Aporrhais vetus Packard, 1922, p. 431, pl. 36, fig. 1

Diagnosis: An *Alarimella* with the outer lip expanded into a broad triangle.



Figures 53–67. All whitened with ammonium chloride. **53–58.** *Alarimella veta* (Packard), hypotypes, **53–54,** USNM 494820 from USGS loc. 2759, ×1, **53,** back view, **54,** labral side showing wing angle, **55–56,** LACMIP 11415 from CIT loc. 978, ×1, **55,** back view, **56,** apertural view, **57,** LACMIP 11416 from CIT loc. 1067, ×1.5, ablabral side, **58,** USNM 494821 from USGS loc. 2759, ×1, apertural view showing channel in wing. **59–67.** *Alarimella anae* n. sp. from CIT loc. 1065, **59–60,** paratype LACMIP 11412, **59,** ×2, back view, **60,** ×1.5, apertural view, **61–62,** paratype LACMIP 11411, ×2, **61,** labral side, **62,** apertural view, **63, 65,** paratype LACMIP 11413, ×3, **63,** back view, **65,** ablabral side, **64,** paratype LACMIP 11414, ×2, apertural view, **66–67,** holotype LACMIP 11410, ×2, **66,** apertural view, **67,** back view.

Description: Shell medium sized, high spired with pleural angle of about 26°; whorl profile on spire flatly convex becoming angulate on ultimate whorl; suture appressed, shallow; body whorl relatively enlarged with a short, straight rostrum; body whorl carina extending onto expanded, triangulate outer lip of nearly equal height and breadth and having a short posterior digitation at its distal margin; posterior edge of outer lip extended upward along spire to form outer, thicked edge of posterior canal; inner lip thickened and extended to form inner edge of canal along spire; interior of outer lip channeled opposite the carina. Sculpture of spire dominated by straight axial ribs, about 16 per whorl, nearly alligned from whorl to whorl, narrower than the interspaces, axial ribs evanescing on apertural side of ultimate whorl but present on back; spiral sculpture of fine cords on spire and about four posterior to carina on ultimate whorl, nearly effaced on mid whorl, becoming stronger anteriorly, about six on base.

Type specimens: Holotype UCBMP 12298.

Hypotypes: LACMIP 11415 from CIT loc. 978 and 11416 from CIT 1067; USNM 494820–494821 from USGS loc. 2759, all in the Santa Ana Mountains, Orange County, California.

Type locality: UCBMP loc. 2171, "4 miles [6.44 km] SW of Corona, Corona Sheet. At clay mine, 200 feet [61 m] up the cañon from a cabin" (Packard, 1922), Riverside County, California.

Dimensions: See Table 9.

Geologic age: Turonian.

Geographic distribution: Upper Baker Canyon

Table 9. Measurements in mm of specimens of *Alarimella veta* (Packard).

	H	Hp	D	Dp	Dp/Hp	S	A	R	Rj	Rp	WB	WH	WD	Whorls
UCBMP 122958	28.3	5.0	13.0	9.8	2.0	14.0	29°	—	—	—	10.7	9.5	9.4	4
USGS 2759-1	36.5†	5.6	29.4	10.9	1.9	16.8†	28°	14	—	16•	16.5	9.8	14.8	5
USGS 2759-2	37.0†	6.4	25.7†	12.4	1.9	16.8†	25°	—		16•	12.0†	8.5	—	4
LACMIP 11415	37.0†	6.5	24.4	10.7	1.6	19.4†	23°	—	—	18•	—	—	—	5
LACMIP 11416	28.9†	5.0	15.0†	8.5†	1.7	12.7	—	14	—	14	8.7†	—	—	4

A = pleural angle; D = diameter last whorl, Dp = diameter of penultimate whorl; H = height; Hp = height penultimate whorl; R = axial ribs on body whorl; Rj = axial ribs on juvenile whorl; Rp = axial ribs on penultimate or other late teleoconch whorl; S = height of spire; WB = wing breadth measured from last rib to distal edge; WD = length distal margin of wing; WH = wing height except posterior and anterior spurs; † = broken, crushed; • = axial ribs counted on one side of whorl and doubled.

Member and lower Holz Shale Member of the Ladd Formation in the Santa Ana Mountains, Orange and Riverside Cos., California (UCBMP loc. 2142, 3 spec.; UCBMP loc. 2171, 1 spec.; USGS loc. 2729, 2 spec.; CIT loc. 1065, 2 spec.; LACMIP loc. 15295, 2 spec.; CIT loc. 979, 2 spec.; LACMIP loc. 10898, 2 spec.; CIT loc. 978, 4 spec.; CIT loc. 1067, 1 spec.

Remarks: Packard (1922) only mentioned the one rather poorly preserved specimen from UCBMP loc. 2171 on the east side of the Santa Ana Mountains, Riverside County, California. He was unsure of the stratigraphic position of this outcrop. Packard (1916) included a sketch map but did not include positions of fossil localities on it. Grey's (1961) map covering the area roughly "4 miles [6.44 km] SW of Corona" indicates that part of the rocks considered Cretaceous by Packard are now mapped as Silverado Formation of Paleocene age. Although many of the clay mines of that area are in strata of Paleocene age, and *Alarimella veta* resembles *Macilentos macilentus* (White, 1889), an early to middle Eocene species (Squires, 1987), no undoubted Paleocene specimens with an expanded outer lip have been found. Furthermore Grey (1961, p. 22) lists *Aporrhais* cf. *A. vetus* from his locality 11 in the Baker Canyon Sandstone Member on the north side of Tin Mine Canyon, sec. 10, T4S, R7W, Corona South quadrangle (Grey, 1961, pl. 1), a locality that is near the southern end of the outcrops of Cretaceous age that are roughly 6.44 km SW of Corona. Specimens of *A. veta* are uncommon but have been collected from several localities in the upper Baker Canyon Member and lower Holz Shale Member of the Ladd Formation in the vicinity of Silverado Canyon, Orange County, California. UCBMP loc. 2142, a locality included in Packard's study, contains several specimens of *A. veta*.

Specimens of *A. veta* lacking the adult apertural characteristics of having a posterior canal up the spire resemble *Latiala nodosa* (Packard, 1922), but they have stronger spiral sculpture than does *L. nodosa*, which also differs from the former in having a slightly more angulate whorl profile with somewhat nodose axial ribs. The wing of *L. nodosa* is taller and has a longer, straighter distal margin with a pronounced anterior projection.

Alarimella veta resembles illustrations of *Calyptraphorus binodiferus* of Maastrichtian age from Guerrero, southern Mexico, in sculpture and shape, but *A. veta* lacks the callus covering of *C. binodiferus*, and *C. binodiferus* lacks the wing of *A. veta*. *Alarimella veta* has stronger sculpture, a shorter posterior canal, and a narrower pleural angle than *C. binodiferus*.

LACMIP 11415 was encrusted on the back of the outer lip and up the spire by calcareous "worm" tubes, and oysters. Tubes are also on the apertural base of the columella, and the shell was bored by sponges. The penultimate whorl has a predepositional hole and the anterior portion of the outer lip has a curved broken edge, both of which suggest that the specimen may have been attacked by a crab.

Table 10. Measurements in mm of specimens of *Alarimella anae* n. sp.

	H	Hp	D	Dp	Dp/Hp	S	A	R	Rj	Rp	WB	WH	WD	Whorls
LACMIP 11410	21.0	3.8	7.7	6.5	1.7	12.4	31°	0?	14	16	8.9	3.9	—	10
LACMIP 11411	17.3†	3.9	9.0	6.8	1.7	8.6†	29°	—	—	16	—	—	—	4
LACMIP 11412	21.8	4.0	7.8	7.4	1.8	—	28°	—	14	16	—	—	—	9
LACMIP 11413	12.0	2.4	5.8	4.0	1.7	—	33°	—	14•	14	—	—	—	5
LACMIP 11414	15.6	2.8	6.4	5.5	2.0	—	33°	—	14•	18•	—	—	—	10

A = pleural angle; D = diameter last whorl; Dp = diameter of penultimate whorl; H = height; Hp = height penultimate whorl; R = axial ribs on body whorl; Rj = axial ribs on juvenile whorl; Rp = axial ribs on penultimate or other late teleoconch whorl; S = height of spire; WB = wing breadth measured from last rib to distal edge; WD = length distal margin of wing; WH = wing height except posterior and anterior spurs; † = broken, crushed; • = axial ribs counted on one side of whorl and doubled.

Alarimella anae n. sp.
Figures 59–67; Table 10.

Diagnosis: An *Alarimella* having a slender posterior spike on the outer lip proximal to the spire, a laterally directed, broad and relatively short wing, and rather coarse axial ribs on the spire.

Description: Shell small, high spired with pleural angle of about 31°; whorl profile on spire slightly convex becoming almost subangulate on ultimate whorl; strong randomly distributed varices present on spire; suture impressed; rostrum apparently short and straight; outer lip expanded into two parts: a posterior short thin spike adjacent at its base to the spire and a larger, carinate, short but broad wing extending laterally; sinus in outer lip margin adjacent to the rostrum; inner lip thin. Sculpture of spire dominated by rounded arcuate axial ribs extending from suture to base, about 16 on penultimate whorl, axial ribs disappearing on back of ultimate whorl and replaced by fine sigmoid axial lines near outer lip that extend onto rostral neck; entire shell surface covered by fine, spaced spiral cordlets.

Type specimens: Holotype, LACMIP 11410; paratypes LACMIP 11411 to 11414 all from CIT loc. 1065.

Type locality: CIT loc. 1065, about 0.97 km north of confluence of Ladd and Silverado Canyons, Black Star Canyon quadrangle, Santa Ana Mts., Orange County, California.

Dimensions: See Table 10.

Age: Late Turonian.

Geographic distribution: Known only from the type locality west of Ladd Canyon, Santa Ana Mountains, Orange County, California, in the Baker Canyon Sandstone Member of the Ladd Formation.

Remarks: *Alarimella anae* may represent early whorls of *A. veta*. The posterior spike adjacent to the spire may be an immature stage of a posterior canal along the spire. The largest specimen of *A. anae* has produced an expanded outer lip and is about half the size of the most complete specimens of *A. veta*. Only one of the nine specimens from CIT loc. 1065 has the wing preserved, and it is thin and fragile. The lip may not be fully mature but its presence suggests that the animal would not be enlarging its shell significantly. Sohl (1960) considers relative size a poor characteristic for specific differentiation among aporrhaids, and both *A. anae* and *A. veta* have about 16 axial ribs per whorl. The ribs of *A. anae* are somewhat more curved and the spiral cordlets are slightly stronger than those of *A. veta*. The fully mature shape of the wing of *A. anae* may differ from that described here. The wing has a slightly curved carina that is nearer to the posterior margin than to the anterior; the anterior side of the wing being about twice as tall as the posterior. Growth lines on the wing clearly conform to the present blade-like shape and suggest that this species had a short but broad, pointed wing.

Alarimella anae resembles illustrations of *Graciliala decemlirata* (Conrad, 1858) of Maastrichtian age from the Ripley and Owl Creek Formations of the Gulf Coast (Sohl, 1960, pl. 11, fig. 5, 11). Young specimens of *A. anae* before the growth of the wing could easily be mistaken for immature *G. decemlirata*, which according to Sohl (1960) is not typical of *Graciliala* in that the anterior border of the outer lip is not digitate. Sohl had no specimens of this species with the wing preserved and could not find Conrad's holotype, but Conrad's illustration (1858, pl. 35, fig. 11) shows a wing slightly taller but similar to that of *A. anae* and, as in *A. anae*, the anterior edge of the outer lip lacked the digitations typical of *Graciliala calcaris* (Wade, 1926) and other species of *Graciliala*.

Alarimella anae differs from *Anchura (H.) tricosa* Saul and Popenoe, 1993, which has a somewhat similar posterior spike, in having fine spiral striae rather than about 5 spiral cords on the spire whorls, fewer axial ribs, and a less angulate whorl profile. The wing of *Alarimella anae* is much shorter, less curved, and is without secondary spurs on the shank. On the ultimate whorl of *A. anae*, the axial sculpture is nearly effaced, and an axial bulge is present on the abapertural side of the apertural face.

Etymology: The specific epithet, *anae*, refers to the name of the Santa Ana Mountains, California.

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LOCALITIES CITED

CIT and UCLA localities have been given LACMIP numbers. The CIT and UCLA numbers for Redding area and Santa Ana Mountains localities are included here because they have been plotted on published maps. Most of the CIT and UCLA localities of Turonian age in the Redding area were plotted on Jones et al. (1978: fig. 5). Most of the CIT localities of the northern Santa Ana Mountains were plotted on Popenoe (1942: fig. 2); these and UCLA localities were plotted on Saul and Bottjer (1982: maps 1–3).

80 CIT = LACMIP 8194: In sandstone above cgl., at fork of Silverado and Ladd Canyons on N side of Silverado Canyon, [NW 1/4, SW 1/4 sec.8, T5S, R7W, El Toro quad.], Santa Ana Mts., Orange County, California. Coll: B. N. Moore, 1926. Ladd Formation, Baker Canyon Sandstone. Turonian.

82 CIT = LACMIP 8195: Limey sandstone bed near base of shale, S of roadcut at Holz's Ranch (locality may become obscured by slides), Silverado Canyon [E edge SE 1/4, SE 1/4, sec.7, T5S, R7W, El Toro quad.], Santa Ana Mts., Orange County, California. Coll: B. N. Moore, 1927. Ladd Formation, Holz-Baker transition. Turonian.

99 CIT = LACMIP 8180: Concretions in shale just above sandstone on south side of Silverado Canyon coming in from south about 1 1/2 miles E of Ladd Canyon [approx. 0.12 km N, 0.07 km E of SW cor. sec.9, T5S, R7W, Santiago Peak quad.], Santa Ana Mtns., Orange County, California. Coll: B. N. Moore, 1928. Ladd Formation, Holz-Baker transition. Turonian.

454 CIT = LACMIP 10873: Cretaceous shale, fireline about Hough's 80 on S side of stream, about 400' above creek, Silverado Canyon [about 450'S, 875'E of NW cor. sec.16, T5S, R7W, Santiago Peak quad.], Santa Ana Mts., Orange County, California. Coll: B. N. Moore, 1929. Ladd Formation, lower Holz Shale. Late Turonian.

978 CIT = LACMIP 10884: NE slope, and near crest of bluff overlooking Santiago Canyon [at about NE cor. sec.33, T5S, R7W], approx. 1 1/2 mi. SE of the dam just above the mouth of Harding Canyon, Santiago Peak quad., Santa Ana Mts., Orange County, California. Coll: W. P. Popenoe, 4/14/1933. Ladd Formation, Baker Canyon Sandstone about 100' above gray basal cgl. Turonian.

979 CIT = LACMIP 10885: 10' below 978, NE slope, and near crest of bluff overlooking Santiago Canyon [at about NE cor. sec.33, T5S, R7W, Santiago Peak quad.], Santa Ana Mts., Orange County, California. Coll: W. P. Popenoe, 4/14/1933. Ladd Formation, Baker Canyon Sandstone, about 90' above gray basal cgl. Turonian.

1058 CIT = LACMIP 10890: North side of Silverado Canyon Road, about 15' above rd., and 300'N 72°E of Holz Ranch house, Silverado Canyon [1390'N, 210'E of SW cor. sec.8, T5S, R7W, El Toro quad.], Santa Ana Mts., Orange County, California. Coll: W. P. Popenoe and others, 4/1/1933. Basal Baker Canyon Sandstone about 10' above top of conglomerate, Ladd Formation. Turonian.

1064 CIT = LACMIP 10893: Area S of Harding Canyon, Vulture Crags, just N of first large canyon cutting across Cretaceous beds S of Harding Canyon, about 2 mi. S42°E of the dam in Harding Canyon and 6800' N55°E of juncture of Santiago Creek and Trabuco Canyon Rds. [2600'N, 1625'E of SW cor. sec.34, T5S, R7W, Santiago Peak quad.], Santa Ana Mts., Orange County, California. Coll: W. P. Popenoe, 10/14/1934. Lower Holz Shale, Ladd Formation. Turonian.

1065 CIT = LACMIP 10891: Ss overlying basal Upper Cretaceous cgl., from crest of scarp on W side of Ladd Canyon, about 0.6 mi. N of juncture of Ladd and Silverado Canyons [1300'S, 300'E of NW cor. sec.8, T5S, R7W, Black Star Canyon quad.], Santa Ana Mts., Orange County, California. Coll: W. P. Popenoe, 3/3/1933. Ladd Formation, Baker Canyon Sandstone. Turonian

1067 CIT: = LACMIP 10883: Immediately above base of gray ss overlying gray basal cgl. [1800'N, 600'E of SW cor. sec.21, T5S, R7W, Santiago Peak quad.], Santa Ana Mts., Orange County, California. Coll: W. P. Popenoe, April 21, 1932. Ladd Formation, Baker Canyon Sandstone Member. Turonian.

1164 CIT = LACMIP 10079: S side Silverado Canyon near mouth of small N-flowing gully, and at top of lower fossiliferous sandstone series, about at top of lower fossiliferous sandstone series, about 400 feet (120 m) SE of Holz Ranch house in SE cor. sec.7, T5S, R7W [1025'N, 150'E of SW cor. sec.8, T5S, R7W, El Toro quad.], Santa Ana Mts., Orange County, California. Coll: W. P. Popenoe, May 15, 1935. Ladd Formation, Baker Canyon Sandstone Member. Turonian.

1212 CIT = LACMIP 10735: Little Cow Creek, ap-

prox. 2 mile (3.2 km) NE of Frazier's Corners, hard sandy concretions in shale, banks of gullies in pasture [about 2500'N, 750'W of SE cor. sec. 4, T32N, R3W, Millville quad.], Shasta County, California. Coll: W. P. Popenoe, 1933. Redding Formation, Frazier Silt. Turonian.

1221 CIT = LACMIP 10738: about 1/4 mi. N of Alturas-Redding hwy U.S. 299 and 1.6 mi. by rd NE of Frazier's Corners, S facing shale bank along Jim Creek [250'S, 700'W of NE cor. sec.8, T32N, R3W, Millville quad.], Shasta County, California. Coll: Popenoe and Ahlroth, June 29, 1936. Redding Formation, upper Frazier Silt Member. Turonian.

1264 CIT = LACMIP 10750: Massive, brown sandstone cropping out in bed of small gully tributary to Little Cow Creek [approx. 1850'S, 2250'E of NW cor. sec.9, T32N, R3W, Millville quad.], Shasta County, California. Coll: W. P. Popenoe, April 12, 1937. Redding Formation, basal Melton Sandstone Member. Turonian

1265 CIT = LACMIP 10751: Right bank of Little Cow Creek, about 50' from creek [0.58 km S, 0.48 km W of NE cor. sec.9, T32N, R3W, Millville quad.], Shasta County, California. Coll: W. P. Popenoe, 4/15/37. Redding Formation, Melton Sandstone Member. Turonian.

1266 CIT = LACMIP 10752: Right bank of Little Cow Creek about 500 ft. downstream from CIT 1265 [center of sec.9, T32N, R3W, Millville quad.,] Shasta County, California. Coll: W. P. Popenoe, April 15, 1937. Redding Formation, Melton Sandstone Member. Late Turonian.

1290 CIT = LACMIP 10135: S side of prominent hill W of Mustang Spring, about 1500' nearly due N of Holz Ranch house, north side Santiago Canyon, sec.7, T5S, R7W, [Black Star Canyon quad.], Santa Ana Mountains, Orange County, California. Coll: Popenoe, Wells, Church, Henshaw, and Fiedler, April 6, 1937. Ladd Formation, near top Baker Canyon Sandstone Member. Late Turonian.

1307 CIT = LACMIP S169: About 25' E of CIT 1290 and not more than 10' stratigraphically below CIT 1290, W of Mustang Spring, north side Santiago Canyon, sec.7, T5S, R7W, [Black Star Canyon quad.], Santa Ana Mountains, Orange County, California. Coll: W. P. Popenoe, April 24, 1937. Ladd Formation, Baker Canyon Sandstone Member. Late Turonian.

1346 CIT = UCLA 5421; LACMIP 10754: Sandstone nodules in shale, left bank of Little Cow Creek, about 70 m NE (upstream) from intersection of creek bed with S line of sec. 9 [1500'N, 2200'E of SE cor. sec.9, T32N, R3W, Millville quad.], 10 mi. NE of Redding, Shasta County, California. Coll: W. P. Popenoe and Jane Hoel, 7/8/1937. Redding Formation, Melton Sandstone Member. Turonian.

1532 CIT = LACMIP 10815: Concretions in shale near right bank Salt Creek [approx. 600'N, 700'W of SE cor. sec.4, T32N, R3W, Millville quad.], Shasta County, California. Coll: Popenoe and Ahlroth, July 10, 1936. Redding Formation, near top Frazier Silt Member. Turonian

2142 UCBMP: 2 1/4 miles NNW of B.M. 1271, Corona sheet. Left side of Silverado Cañon, in shales undercut by the stream about 200 ft. southeast of the road. Ladd Formation, lower Holz Shale Member. Turonian

2171 UCBMP: 4 miles SW of Corona, Corona Sheet [Corona South quad.]. At clay mine, 200 feet up the cañon from a cabin, Riverside County, California. Ladd Formation. Turonian.

2325 UCLA = LACMIP 22325: Small gully entering Silverado Canyon from S, just W of the narrows, about 9000' upstream from the mouth of the canyon, and directly S from farmhouse on Holz Ranch, about 1025'N, 150'E of SW cor. sec.8, T5S, R7W, El Toro quad., Santa Ana Mts., Orange County, California. Coll: W. P. Popenoe, 1946. Ladd Formation, top of Baker Canyon Member. Turonian.

2759 USGS: Near Silverado Canyon, in lower part of Ladd Canyon, Santa Ana Mountains Orange County, California. Coll: S. Bowers, April 24, 1903. Ladd Formation, Baker Canyon Sandstone Member. Turonian.

3465 UCLA = LACMIP 23465: Fossils in small knob of sandy cgl., on North Fork of Cottonwood Creek, about 1500'SSW of UCLA 3464, 0.38 mi. N, 0.3 mi. E of SW cor. sec.16, T30N, R6W, Ono quad., Shasta County, California. Coll: P. U. Rodda and M. A. Murphy, May 1955. Budden Canyon Formation, Bald Hills Member. Late Cenomanian.

4365 UCLA = LACMIP 24365: In fine grained ss with *Romaniceras*, left bank of French Creek (north end Swede Basin), approx. 500'N and W of SE cor. sec.5, T32N, R2W, Millville quad., Shasta County, California. Coll: W. P. Popenoe, 8/25/1957. Redding Formation, basal bed of ?Frazier Siltstone, Turonian.

4658 UCLA: Concretions at top of Frazier Siltstone, right bank of Salt Creek, about 1000'N, 400'W of SE cor. sec.4, T32N, R3W, Millville quad., Shasta County, California. Coll: W. P. Popenoe, Aug. 1961. Redding Formation, Frazier Siltstone Member, Turonian.

5421 UCLA = LACMIP 25421: Sandstone nodules in shale, left bank of Little Cow Creek, about 5' above the channel bottom, about 70 m NE (upstream) from intersection of creek bed with line fence, and about 1/4 mi. downstream from old Walter Melton farmhouse [S line sec.9, T32N, R3W, Millville quad.], Shasta County, California. Coll: W. P. Popenoe, summer, 1937.

Redding Formation, Melton Sandstone. Turonian.

10876 LACMIP = CIT 1042: Limey lenses in ss cropping out on N bank of Rancheria Gulch, about 1.5 mi. W of Henley [approx. 210'S, 800'E of NW cor. sec.30, T46N, R6W, Hornbrook quad.], Siskiyou County, California. Coll: Popenoe and Findlay, Sept. 8, 1933. Hornbrook Fm., Osburger Gulch Sandstone Member. Turonian.

10895 LACMIP: North side of Harding Canyon, north of Modjeska Reservoir, at elev. 1705', 1775'N, 1075'E of SW cor. sec.21, T5S, R7W, Santiago Peak quad., Santa Ana Mts., Orange County, California. Coll: L. J. Czel, spring 1958. Ladd Formation, Baker Canyon Sandstone Member. Turonian.

10898 LACMIP: North side of Harding Canyon, north of Modjeska Reservoir, at elev. 1750', 950'N, 600'E of SW cor. sec.21, T5S, R7W, Santiago Peak quad., Santa Ana Mts., Orange County, California. Coll: L. J. Czel, spring 1958. Baker Canyon Sandstone, Ladd Formation. Turonian.

10901 LACMIP = CIT 1044: Right bank of Rancheria Gulch just over hill north from Scholz Ranch house, 1.5 mi. W of Henley, 535'S, 1435'W of NE cor. sec.30, T47N, R6W. Yreka quad., Siskiyou County, California. Coll: W. P. Popenoe and W. A. Findlay, Sept. 1933. Hornbrook Fm., Osburger Gulch Sandstone Member. Turonian.

10953 LACMIP: Holz Ranch, north side of Silverado Canyon, on ridge top west of Ladd Canyon at approx. 1510' elev., approx. 197' above base of upper Baker Canyon Sandstone, 2550'N, 520'E of SW cor. sec.8, T5S,. R7W, Black Star Canyon quad., Santa Ana Mts., Orange County, California. Coll: R. G. Cassi, spring 1958. Ladd Formation, upper Baker Canyon Member. Turonian.

15295 LACMIP: South side of Silverado Canyon near mouth of small N-flowing gully, about 400' SE of Holz Ranch house, 1025'N, 150'E of SW cor. sec. 8, T5S, R7W, El Toro quad., Santa Ana Mts., Orange County, California. Coll: Robert Drachuk, 1979. Top of Baker Canyon Sandstone Member, Ladd Formation. Turonian.

16838 LACMIP: Float—North Fork of Cottonwood Creek, 3/4 mi. downstream from mouth of Huling Creek, Sec.21, T30N, R6W, Ono quad., Shasta County, California. Coll and date unknown. Budden Canyon formation. Bald Hills Member. Cenomanian.

24370 LACMIP (=CIT 1020; UCLA 4370): Sandstone boulder in heavy conglomerate, channel of Elder Creek, about 0.8 mi. N and E of SW cor. sec.14, T25N, R6W, at east edge of Colvear Springs quad., Tehama County, California. Coll: W. P. Popenoe and W. A. Findlay, August 18, 1933. Great Valley Series, Budden Canyon Formation. Cenomanian or late Albian boulder in Turonian sandstone.

24670 LACMIP = UCLA 4670: Sandstone cropping out in bed and on west bank of Grave Creek, W of road, 2400'N of SW cor. sec.5, T34S, R4W, Wimer 1954 15' quad., Jackson County, Oregon. Coll: W. P. Popenoe, Aug. 20, 1960. Late early–middle Albian.

25422 LACMIP = UCLA 5422: Rancheria Gulch, about 1 mi. W of Henley, and approx. 400'N, 2000'W of SE cor. sec.19, T47N, R6W, Yreka 30' quad. (1939), Siskiyou County, California. Coll: W. P. Popenoe, summer 1951. Hornbrook Formation, Osburger Gulch Member. Turonian.

28788 LACMIP: (=USGS loc. 14528) boulder in cgl., NW end of McLure Valley = Sunflower Valley, elev. 1420', 1250'N, 775'W of SE cor. sec.20, T23S, R17E, Reef Ridge quad., Kings County, California. Coll: Ralph Stewart. Panoche Formation. Cenomanian.

29181 LACMIP: Hill north of Holz Ranch house at about 1500' elev., sec. 8, T5S, R7W, Black Star Canyon quad., Santa Ana Mts., Orange County, California. Coll: W. P. Popenoe. Ladd Formation, Baker Canyon Sandstone Member. Turonian.

Salinity Tolerance of the Freshwater Bivalve *Dreissena polymorpha* (Pallas, 1771) (Bivalvia, Dreissenidae)

Shawn J. Wilcox
Thomas H. Dietz[1]
Department of Biological Sciences
Louisiana State University
Baton Rouge, LA 70803, USA

ABSTRACT

The effects of elevated ion concentrations in the bathing medium on osmoregulation and mortality rates were examined in the freshwater bivalve *Dreissena polymorpha*. Animals acclimated to artificial pondwater (APW) tolerated an acute transfer to approximately 100 mosmol kg^{-1} artificial seawater (3.5‰ ASW), for months, with virtually no mortality. However, there was substantial mortality, within days, when the animals were acutely transferred to dilute ASW greater than 150 mosmol kg^{-1} (5‰). *Dreissena polymorpha* rapidly (~12 h) became isosmotic to the bathing medium when exposed to 100 mosmol kg^{-1} ASW, although it took 3 d of acclimation before the ion concentrations in the blood stabilized. Salinity tolerance was increased when the animals were acclimated for 3 d to a salinity of 54 mosmol kg^{-1} ASW followed by 54 mosmol kg^{-1} salinity increases every third day. Although some mussels acclimated for 2 weeks to 377 mosmol kg^{-1} ASW could survive direct transfer to APW, survival was improved when the acute reduction in salinity was less than 260 mosmol kg^{-1}. *Dreissena polymorpha* has the capacity to tolerate oligohaline water with small fluctuations in salinity.

Key words: zebra mussel, estuary, salinity tolerance, fresh-water bivalve, ion regulation, osmoregulation.

INTRODUCTION

Dreissena polymorpha require minimal concentrations of Mg^{2+}, Na^+, Cl^- and K^+ in the bathing medium to ionoregulate (Nichols, 1993; Ram & Walker, 1993; Dietz *et al.*, 1994). *Dreissena polymorpha* cannot survive a week when 45 mmol l^{-1} NaCl is added to artificial pondwater (APW), or survive one day if the K^+ concentration is increased to 1 mmol l^{-1} (Horohov *et al.*, 1992; Fisher *et al.*, 1991). However, these animals will survive in dilute artificial seawater (Kilgour *et al.*, 1994; Wright *et al.*, 1996; Dietz *et al.*, 1997), and have been observed in brackish water and in estuaries where ambient salinities range from freshwater to greater than 12‰ (Aladin & Potts, 1992; Klimowicz, 1958; Strayer & Smith, 1993).

[1] Author for correspondence.
E-mail: zothom@lsuvm.sncc.lsu.edu

The effects of environmental perturbation (temperature, salinity) on the physiological processes associated with ion regulation and salinity tolerance have been studied recently (Dietz *et al.*, 1994; Kilgour *et al.*, 1994; Scheide & Bonaminio, 1994; Wright *et al.*, 1996). Some reports suggest that the salinity tolerance of *D. polymorpha* from North American populations is influenced by multiple factors including temperature, life stage and the salinity acclimation regime (Kilgour *et al.*, 1994; Wright *et al.*, 1996). Recently, we have observed that mussels exposed to elevated Na^+ and K^+ (~10% seawater) will redistribute the ions between the intracellular (ICF) and extracellular fluid (ECF) compartments (Dietz *et al.*, 1997). When both Na^+ and K^+ are present in the media, the mussels maintained a normal ICF/ECF K^+ ratio. In addition, the epithelial cells in the gill were able to partially recover cellular volume when exposed to a hyperosmotic bath containing 45 mmol l^{-1} Na^+ and 1 mmol l^{-1} K^+, but could not do so when K^+ was absent (Dietz *et al.*, 1998).

In this study we report the effects of osmotic and ionic challenges on body fluid ion concentrations and survival in *D. polymorpha*. We identify the environmental salinity limits and changes that are compatible with osmoregulation and survival.

MATERIALS AND METHODS

Animals: Specimens of *Dreissena polymorpha* (zebra mussels) were collected from Lake Erie at the mouth of the Raisin River in Michigan and from the Mississippi River near Baton Rouge, Louisiana. Mussels were stored unfed in aquaria containing aerated artificial pondwater (APW in mmol l^{-1}; 0.5 NaCl, 0.4 $CaCl_2$, 0.2 $MgSO_4$, 0.2 $NaHCO_3$, 0.05 KCl; Dietz *et al.*, 1994). Some of the animals were kept at 13°C and were step-wise acclimated to 16°C and 22 ± 2°C for >5 d at each temperature before use. Only large animals (1.5–3 cm shell length) attached to the container or to another mussel by byssal threads were used. Aquarium water was replaced every 2–3 d and waste water and containers were treated with 1% chlorine bleach.

Solute analyses: Blood samples (150–200 µl) were collected by pericardial puncture from individual mussels and centrifuged at 15,000 g min before analysis (Fyhn & Costlow, 1975). The osmolality of the blood was determined by freezing point depression. Sodium and potassium concentrations were determined by flame emission photometry on diluted samples. Calcium and magnesium samples were diluted with $LaCl_3$/HCl and assayed using an atomic absorption spectrophotometer. Chloride was determined by electrometric titration. The difference between the total solute of the blood and the sum of the measured ion concentrations was identified as "other" and is mostly bicarbonate in APW acclimated animals (Byrne & Dietz, 1997), but sulfate is a significant component in ASW (Potts, 1954; Withers, 1992). Net ion flux (J_{in}) was determined by measuring the change in bathing fluid ion concentration at specific intervals. The flux was expressed as µmol g^{-1} dry tissue h^{-1}.

Elevated bath solute concentrations: Some mussels were either acutely exposed or step-wise acclimated to a modified artificial seawater (ASW) diluted with APW (ASW in mmol l^{-1}; 449.1 NaCl, 27.5 $MgSO_4$, 24.4 $MgCl_2$, 9.9 $CaCl_2$, 6.6 KCl, 2.4 $KHCO_3$, 0.8 KBr, 0.4 H_3BO_3; 1076 mosmol kg^{-1} total solute concentration; 35‰; Chambers & De Armendi, 1979). No buffer was added to the seawater stock and the pH in diluted samples varied from 7–8. The artificial seawater was diluted with APW to approximate natural mixtures of freshwater and seawater.

We determined the effects of an acute transfer to elevated salinity on the blood ion composition and mortality in mussels. Animals were transferred directly from APW to a bath of diluted ASW that was changed daily. We calculated (see below) the time to 50% mortality (LT_{50}) and recorded the time of death of the last animal as 100% sample mortality (SM_{100}). The animals used for chronic exposure to a constant bath salinity concentration were exposed to 54 mosmol kg^{-1} ASW for 3 d followed by subsequent increases of 54 mosmol kg^{-1} at 3 d intervals until the specified bath solute concentration was attained, and the salinity held constant thereafter.

Animals were exposed to cyclic changes in salinity by adding 9 liters of 161 mosmol kg^{-1} ASW from a Mariott bottle, over 12 h, to one liter of APW resulting in bath concentration of 130 mosmol kg^{-1} ASW. After 12 h all but one liter of the bath was discarded and nine liters of APW was added over 12 h to return the salinity to about 14 mosmol kg^{-1} After 6 d of the salinity cycles, samples of bathing medium and blood from 5 animals were collected at 4 h intervals for 24 h.

Mortality studies: We determined the ability of *D. polymorpha* to tolerate acute transfer to dilutions of ASW by noting their survival time and recording behavioral changes. Animals that gaped widely, were unresponsive to stimulation by touching the valves or tissue near the siphons, and did not hold the valve closed when mechanically closed with forceps, were considered dead and the time noted. Some of the animals acclimated to hyperosmotic solutions and acutely transferred to hyposmotic solutions appeared to swell and were unable to completely close the valves, but we were able to determine live or dead animals reliably by judging motor activities. The time for 50% sample mortality (LT_{50}) was calculated from a probit model (Finney, 1971), using a linear regression of the logarithm of time and cumulative mortality: probit (% dead) = A + B (log time, h or d).

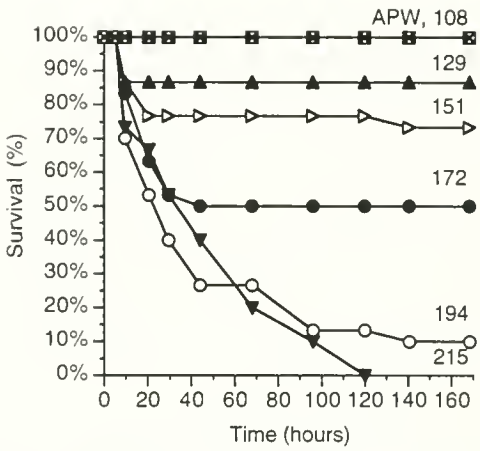

Figure 1. Percent survival of APW-acclimated *D. polymorpha* acutely transferred to artificial seawater diluted with APW (N = 30 for each group). The number adjacent each line represents the total solute, in mosmol kg^{-1} measured in the bathing medium.

Statistical analyses: Data are expressed as mean ± s.e.m. Data were tested for homogeneity of variance and some of these data were log transformed before one-way analyses of variance (ANOVA) were performed at an alpha level of 0.05. A treatment that had a significant ANOVA was examined for similarities and differences using the Tukey Studentized range procedure at an alpha level of 0.05 (equal sample sizes), or with the Tukey-Kramer modification when sample sizes were unequal (SuperANOVA, Abacus Concepts Inc., Berkeley, California).

RESULTS

Acute transfer to dilute artificial seawater: APW-acclimated *D. polymorpha* transferred directly into dilute ASW with solute concentrations greater than 151 mosmol kg^{-1} (5‰) suffered substantial mortality between 5 and 21 h (Fig. 1). The LT_{50} was ~31 h for animals transferred to 215 (7‰) and about 36 h for animals in 194 (6.3‰) mosmol kg^{-1} ASW. Survival time increased (LT_{50} 74 h) for the animals transferred to 172 mosmol kg^{-1} (5.6‰) ASW. The experiment was terminated after 2 weeks and LT_{50} values were not determined for the four groups in salinities ≤151 mosmol kg^{-1} as all or the majority of the animals survived. Mussels acclimated <108 mosmol kg^{-1} ASW survived for months (LT_{50} 3–4 mo), unfed, as did the APW-acclimated control animals (LT_{50} 4–5 mo). A majority of the an-

Table 1. Changes in *Dreissena polymorpha* blood ion concentrations following acute transfer to 108 mosmol kg^{-1} ASW (3.5‰).

Time (h)	N	mosmol kg^{-1}		Concentration (mmol l^{-1})				
		*Total solute	Other	Na^+	Cl	K^+	Ca^{2+}	*Mg^{2+}
0	5	49 ± 3[d]	11.0 ± 1.7[a]	18.5 ± 1.1[c]	14.4 ± 0.4[c]	0.6 ± 0.1[c]	4.0 ± 0.1[a]	0.5 ± 0.0[c]
12	7	85 ± 2[c]	4.2 ± 1.7[b]	38.8 ± 1.1[b]	36.4 ± 0.8[a,b]	0.8 ± 0.0[c]	2.3 ± 0.2[b]	2.9 ± 0.1[b]
24	6	97 ± 1[b]	10.1 ± 1.7[a]	40.5 ± 0.7[a,b]	34.1 ± 0.5[b]	1.2 ± 0.1[b]	2.0 ± 0.1[b]	5.5 ± 0.1[a]
72	6	102 ± 1[a]	13.2 ± 1.4[a]	42.4 ± 0.9[a]	37.3 ± 0.6[a]	1.6 ± 0.1[a]	2.5 ± 0.1[b]	5.1 ± 0.1[a]

Mean ± sem. "Other" was calculated from the difference between the total solute and measured ion concentrations. Means within a column with different letters are significantly different by the Tukey-Kramer Studentized range procedure, $P < 0.05$; (*) log transformed data for statistical analyses.

imals in <108 mosmol kg^{-1} ASW formed byssal thread attachments within 48 h of the transfer.

Changes in blood solute concentration: *Dreissena polymorpha* transferred from APW to 108 mosmol kg^{-1} ASW became isosmotic with the bathing medium between 12 and 24 h (Table 1). Sodium concentration in the blood rapidly tended to become isoionic, but Cl^- remained hypoionic to the medium. Although the ASW bath contained elevated Ca^{2+} and Mg^{2+} compared to APW, the blood concentration of Ca^{2+} decreased 40–50%, but the Mg^{2+} rose 10-fold and became isoionic with the bath.

Exposure to elevated artificial seawater concentrations: *Dreissena polymorpha* suffered considerable mortality when acutely transferred to salinities approaching 15‰ ASW, but tolerated more dilute solutions. Therefore, we examined the ability of mussels to survive a step-wise increase in salinity then subsequently held at a constant salinity. Several hundred mussels were transferred to 54 mosmol kg^{-1} (1.5‰) for 3 d and the salinity was increased by 54 mosmol kg^{-1} at 3 day intervals. At several salinities ranging from 269 to 486 mosmol kg^{-1} groups of 30 mussels were transferred to separate containers. The water was changed daily, but the salinity was held constant thereafter and the survival was monitored (Table 2). The LT_{50} for the mussels was inversely related to the concentration of the final bathing solution. However, the total length of time mussels tolerated both the step-wise salinity adjustment and constant salinity acclimation to reach the LT_{50} ranged from 29 to 47 d, with no consistent pattern. We typically observed greater than 97% survival up to 269 mosmol kg^{-1} (8.8‰) in large groups of mussels (~300) during the step-wise adjustment in salinity. These data have some bias since the most tolerant animals survived the step-wise salinity change and were used to determine the LT_{50}. In three separate studies, >70% of the mussels survived the step-wise increase in salinity up to about 380 mosmol kg^{-1}

Table 2. Survival (LT_{50}) of *Dreissena polymorpha* chronically exposed to dilutions of artificial seawater.

Final bath solute concentration (mosmol kg^{-1})	Pre-acclimation time (days)	Days LT_{50}
269	12	30.5
325	15	21.3
377	18	14.7
486	24	5.4

The pre-acclimation time was the total number of days the animals were in step-wise increasing salinity (54 mosmol kg^{-1} at 3 day intervals) until the specified final bath concentration was established. The LT_{50} was determined on 30 animals at each salinity.

Diurnal salinity changes: Because the salinity of oligohaline water in coastal environments tends to change in a cyclic manner, we examined the ability of *D. polymorpha* to tolerate cyclic changes in salinity. We exposed the mussels to diurnal changes in salinity ranging from 14 to 130 mosmol kg^{-1} for over a week and all of the animals survived and formed byssal attachments. The blood ion composition of the mussels paralleled the bathing medium during both the dilution and increasing salinity phases of the cycle (Fig. 2). The blood ion composition and concentrations lagged approximately 2–4 h behind the changes in the ion composition of the bath. The mussel blood became isosmotic to the bathing medium during the high salinity phase of the cycle. During the initial 4 h of the dilution phase the total solute in the blood decreased rapidly, but the mussels osmoregulated in the lower salinities. The concentrations of the measured ions also decreased as the bath became dilute, but the concentration of unidentified osmolytes (other) was elevated. The control animals held in constant dilute ASW or APW maintained constant blood ion composition during the 8 d. In a similar study, we extended the tidal cycle for 11 d and all of the animals survived (data not shown). Most of the animals attached by byssal threads within 48 h in both experiments.

Acute transfer from hyperosmotic to hyposmotic media: We analyzed the blood ion concentration of animals that survived 14 d acclimation to constant 377 mosmol kg^{-1} seawater and for 24 h after being returned to APW (Table 3). Animals that were acutely transferred to APW experienced a 79% reduction of the blood total solutes within 6 h (Table 3). The restoration of blood ion composition was not completed within 24 h as only the concentration of Ca^{2+}, K^+, and total solute

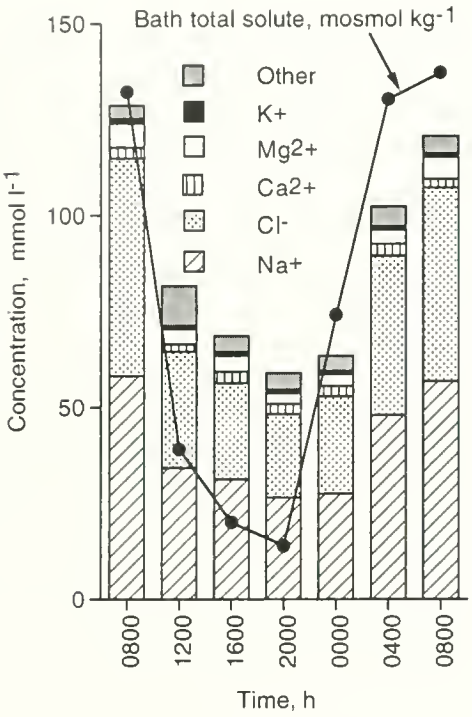

Figure 2. The changes in blood ion composition of *D. polymorpha* over a 24 h salinity cycle ranging from 14 to 130 mosmol kg^{-1} solute (N = 5). The animals were exposed to the diurnal changes in salinity for 6 d and blood samples collected during day 7. The individual ion concentrations in the blood were added to form the stacked histogram. The filled circles represent the total solute concentration in the bath at the respective blood sampling times.

were similar to APW control animals. The concentrations of Na^+ and Cl^- were significantly less than controls, but Mg^{2+} and the unmeasured solutes (other) remained elevated. It was likely that the decline in solute concentrations was due to both the osmotic uptake of water as well as a loss of ions to the environment, but these variables were not measnred during this study (see Dietz *et al.*, 1997). In a separate study we measured net ion losses when mussels were directly transferred from 106 mosmol kg^{-1} ASW to APW. The animals lost Na^+, Cl^-, and K^+ ions exponentially to the bathing medium during the initial 18 h in APW [regression coefficients (R) for Na^+, 0.998; Cl^-, 0.999; K^+, 0.994; $P < 0.05$ all regressions]. During the flux study, the average net flux of ions was: Na^+ $J_n = -66.6 \pm 8.1$; Cl^- $J_n = -74.6 \pm 10.9$; K^+ $J_n = -7.5 \pm 0.6$ μmol g^{-1} dry tissue h^{-1} ($N = 5$). The total solute of the blood returned to values similar to APW controls by 43 h.

There was substantial mortality (50% in 48 h) when the animals were transferred from 377 mosmol kg^{-1} seawater to APW, but similar groups of animals transferred to 161 and 108 mosmol kg^{-1} ASW tolerated the hyposmotic stress (>70% survival after 21 d). These animals rapidly became isosmotic to the new solute concentration in the bath in 12 h (data not shown). In a similar experiment, animals acclimated for 14 d to constant 269 mosmol kg^{-1} seawater were transferred into hyposmotic bathing media (APW, 108 and 161 mosmol kg^{-1} ASW) and we observed a similar rapid reduction in blood ion composition within 12 h, but survival increased (>83% after 3 weeks) even in those animals transferred directly to APW.

DISCUSSION

An acute transfer of APW-acclimated *D. polymorpha* to 172 mosmol kg^{-1} was lethal to half of the animals in 3 d. The observed intolerance was likely due to the limited ability of these animals to control the rapid rate of water and solute movement between the environment and animal body fluid compartments. This inference is supported by the observation that *D. polymorpha* survived step-wise acclimation to salinity when the change was limited to increments of 54–108 mosmol kg^{-1}. Small changes in salinity and 1–3 d of acclimation between changes allowed the animals to survive salinities approaching 269 mosmol kg^{-1} before the onset of substantial mortality (Kilgour *et al.*, 1994; Wright *et al.*, 1996; this study).

The response of *D. polymorpha* to elevated salinity was to osmoconform. The isosmotic condition is accomplished by the accumulation of salts, and partially by the osmotic loss of water (Dietz *et al.*, 1997). The intracellular fluid compartment is subject to limited regulation.

Table 3. The blood ion composition of *Dreissena polymorpha* acclimated to 377 mosmol kg^{-1} artificial seawater for 14 days and acutely transferred to artificial pondwater (APW).

		mosmol kg^{-1}		Concentration (mmol l^{-1})				
Bathing medium	N	Total solute	Other	*Na^+	*Cl	K^+	Ca^{2+}	*Mg^{2+}
APW controls	5	39 ± 1[a]	2.1 ± 0.7[b]	16.7 ± 0.6[a]	15.2 ± 0.6[a]	0.5 ± 0.0[a]	3.9 ± 0.3[a]	0.4 ± 0.1[d]
377 mosmol kg^{-1}	5	386 ± 2[c]	−13.3 ± 4.5[a]	170.3 ± 2.0[c]	206.8 ± 4.7[c]	5.2 ± 0.1[c]	4.6 ± 0.2[a]	12.5 ± 0.2[a]
APW, 6 hr	4	83 ± 3[b]	14.2 ± 2.3[a]	28.2 ± 2.5[b]	33.8 ± 0.8[b]	1.0 ± 0.1[b]	2.7 ± 0.2[b]	3.0 ± 0.3[b]
APW, 24 hr	4	40 ± 1[a]	14.0 ± 1.5[a]	10.5 ± 0.5[d]	9.2 ± 1.7[d]	0.5 ± 0.1[a]	4.6 ± 0.4[a]	1.1 ± 0.0

Mean ± sem. "Other" was calculated from the difference between the total solute and measured solutes. The negative "other" is due to complete ionization of NaCl and Ca^{++} salts when diluted for individual ion analyses. Means within a column with different letters are significantly different by the Tukey-Kramer Studentized range procedure, $P < 0.05$; (*) log, transformed data for statistical analyses.

These mussels have some ability to preserve the ICF and make adjustments to cellular volume when they are hyperosmotically challenged (Dietz *et al.*, 1997; 1998). However, only mussels exposed to saline solutions containing sufficient K^+ are able to maintain the ICF/ECF potassium gradient (Dietz *et al.*, 1997). Previous studies have demonstrated that potassium availability in the environment apparently is critical for preserving the intracellular volume, electrochemical balance, and survival (Dietz *et al.*, 1994; Dietz *et al.*, 1997). *Dreissena polymorpha* is similar to other freshwater bivalve species in that an increase in concentration of specific ions in the bathing medium results in a concomitant increase in the concentration of that ion in the blood (Deaton & Greenberg, 1991; Horohov *et al.* 1992; Wilcox & Dietz, 1995).

A change in ASW of ~100 mosmol kg^{-1} at 3 d intervals allowed sufficient time for the animals to acclimate. This observation contrasts with an earlier study where *D. polymorpha* could not survive a week when 45 mmol l^{-1} NaCl was added to the APW (Horohov *et al.*, 1992). *Dreissena polymorpha* is the least tolerant of the freshwater bivalves when challenged with hyperosmotic medium of NaCl. In contrast, when the medium contains 45 mmol l^{-1} NaCl and approximately 1 mmol l^{-1} KCl, the hyperosmotic challenge is tolerated by this species (Dietz *et al.*, 1997; this study). *Dreissena polymorpha* will accumulate K^+ in the intracellular and extracellular fluid compartments from the bathing medium (Dietz *et al.*, 1997; 1998). The potassium allows limited cellular volume regulation that likely contributes to the animal survival in hyperosmotic conditions.

Volume regulation in euryhaline and stenohaline bivalve species is, in part, dependent on the rate of change of the free amino acid pool in response to a short-term osmotic challenge (Deaton & Greenberg, 1991; Silva & Wright, 1994; Neufeld & Wright, 1996). An acute transfer to a salinity of about 100 mosmol kg^{-1} caused virtually no short-term mortality in *D. polymorpha*. Salinities between 120 and 150 mosmol kg^{-1} were at the tolerance limit for an acute exposure for this species. However, freshwater bivalves depend primarily on electrolytes for volume regulation as they have relatively low concentrations of free amino acids (Hanson & Dietz, 1976; Potts, 1958; Dietz *et al.*, 1997). Although the free amino acid concentration is elevated with hyperosmotic challenge, it is a minor class of intracellular osmolytes in freshwater bivalves (Potts, 1958; Dietz *et al.*, 1997).

When mussels were exposed for a week to a diurnal cycle of salinity change of 14 to 130 mosmol kg^{-1}, they repeatedly gained or lost ions from the blood depending on the direction of salinity change. Most of the ion flux at higher ion concentration gradients was attributed to diffusion (see Wilcox & Dietz, 1995; Dietz *et al.*, 1997). Thus, the changes in body fluid solute concentrations with salinity cycles would be largely passive diffusion. In APW the mussels would be required to expend energy for osmoregulation, but less energy is expended as the animals osmoconform. Shumway (1977) observed that the tissue water content in *Mytilus edulis* remained relatively constant during exposure to a sinusoidal full strength seawater/freshwater tidal cycle for 7 d. It was suggested that animals exposed to an environment of constantly fluctuating salinity would not continuously conform to the external salinity but instead, maintain a tissue hydration level that required the least amount of energy expenditure.

Dreissena polymorpha acclimated to 377 mosmol kg^{-1} and transferred to APW lost ions and appeared to undergo a transient swelling due to osmotic water uptake. The reduction in ion concentration in the blood following transfer to APW was evident within 6 h, but the animals had not returned to control conditions by 24 h, as the concentrations of some ions were above and below those found in APW-acclimated controls. Many specimens could not tolerate the acute decrease in osmolality of 370 mosmol kg^{-1} as 50% of the animals died in 48 h. In contrast, the brackish-water bivalve, *Corbicula japonica*, is capable of surviving the transition from 425 mosmol kg^{-1} seawater directly to freshwater with blood total solute concentration returning toward control levels within a day (Matsushima, 1982).

Several bivalve species exhibit a distinct hypercalcemia upon exposure to dilute media and the response is inversely correlated with an increasing tolerance to freshwater (Deaton & Greenberg, 1991). The Ca^{2+} in the blood of *D. polymorpha* acclimated to elevated salinity, initially dropped upon acute exposure to APW, but was restored within 24 h to a concentration that was equal to that found in animals acclimated to APW (Table 3). These animals likely supplement the Ca^{2+} concentration in the blood with endogenous Ca^{2+} sources (shell). However, *D. polymorpha* blood Ca^{2+} concentration changed very little with values ranging between 2 and 4.6 mmol l^{-1} under the conditions used in this study. This species does not appear to utilize Ca^{2+} as a significant extracellular osmolyte, but does regulate the concentration within narrow limits. There appears to be a reciprocal relationship between the concentrations of Ca^{2+} and Mg^{2+} in the blood *of D. polymorpha*. Magnesium was poorly regulated at the higher concentrations found in dilute ASW, but was hyper-regulated by the animals acclimated to APW (Dietz *et al.*, 1994).

Dreissena polymorpha appears to be a freshwater mussel in transition from its brackish water ancestry. These animals evolved in freshwater connected to inland seas having minimal diurnal salinity changes. The apparent euryhalinity of *D. polymorpha* suggests that these bivalves have some capacity to tolerate oligohaline habitats. However, this species will likely be restricted to low salinity environments that have slowly changing salinity cycles. *Dreissena polymorpha* are not likely to tolerate habitats with rapid and large salinity fluctuations associated with daily tidal cycles.

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Notices

UPCOMING MEETINGS, CONVENTIONS, AND WORKSHOPS

1998 Annual Meeting of the North American Benthological Society, Charlottetown, Prince Edward Island, Canada, 2–5 June 1998. Contact: Dr. Jill Lancaster, j.lancaster@ed.ac.uk

1998 Conchologists of America Convention, Orlando, Florida, USA, 19–23 July 1998. Local contact: Linda Koestel, lkoestel@magicnet.net

1998 World Congress of Malacology, Washington, DC, USA, 25–30 July 1998. Combining the 13th International Congress, Unitas Malacologica, and 64th Annual Meeting, American Malacological Union together with other participating malacological organizations. Local contact: Dr. Robert Hershler, hershler.robert@nmnh.si.edu

The 8th International Congress on Invertebrate Reproduction and Development (ICIRD), Amsterdam, The Netherlands, 10–15 August 1998. Contact: VU_conference@dienst.vu.nl

Global Biodiversity Forum, 29–31 August 1998, Montreal, Canada. Contact: celias@wri.org

III Symposium "Fauna and Flora of the Atlantic Islands", Ponta Delgada, Azores Islands, Portugal, 21–25 September 1998. Contact: simposio@alf.uac.pt

Annual Meeting of the Society of Integrative and Comparative Biology (formerly The American Society of Zoologists), Denver, Colorado, USA, 6–10 January 1999. Held jointly with The American Microscopical Society and The Crustacean Society meetings. Contact: corinne_o'brien@sba.com

Annual Meeting of the Society for Conservation Biology, College Park, Maryland and Washington, DC, USA, 17–21 June 1999. Local contact: David Inouye, di5@umail.umd.edu

IV Congreso Latinoamericano de Malacologia, Coquimbo, Chile, 1999. Local contact: Dr. Chita Guisado, cguisado@nevados.ucn.cl

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